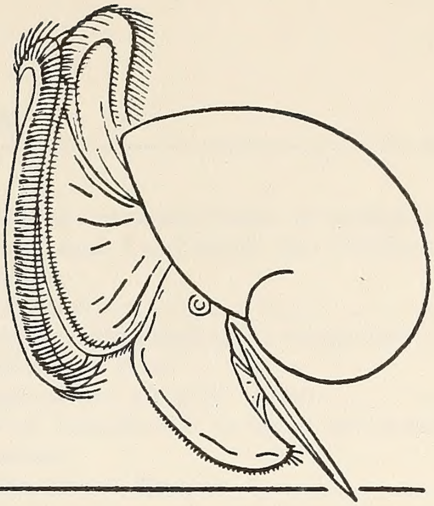
THE VELIGER



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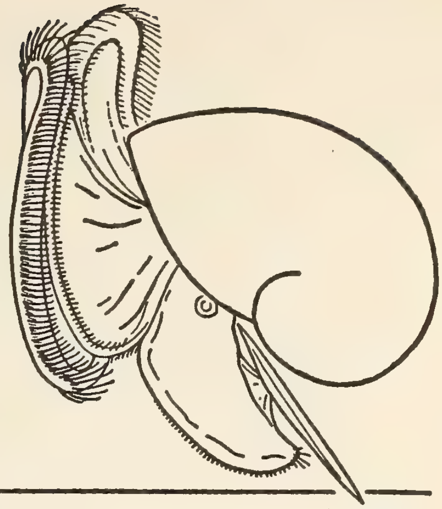

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, **DIVISION**, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

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The Comparative Morphology and Evolution of the Molluscan Mantle Edge

BY

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(13 Text figures)

INTRODUCTION

IN A RECENT EVALUATION of the probable course of molluscan evolution Stasek concurred with LANG (1896) in viewing the phylum as descended from free-living flatworms that were dorsally covered by a cuticle (STASEK, 1972). This cuticle was the precursor of the calcified shell characteristic of the higher Mollusca and, together with trends toward increase in size, was the evolutionary factor responsible for the subsequent appearance of most of the other anatomical features that distinguish the group as a phylum.

The rationale underlying that idea is that the cuticle, and its later elaboration as a shell, developed in relation to protection, but inhibited locomotion and diffusion of respiratory gases. The open circulatory system with hemocoelic sinuses, pumping heart, "coelom," and gills all evolved in relation to improved respiratory function. It was in relation to augmented protection and to increased facility of locomotion that the sides of the body and cuticle became extended as eaves beyond the body proper. These lobes functionally released the body from the edges of the cuticle or shell, thereby increasing freedom of movement, especially turning of the organisms. The mantle lobes, mantle cavity, and foot, all basic qualities of the molluscan framework, are the topographic results of this development.

The dorso-ventral muscles of the antecedents became the pedal retractor muscles of the mollusks, with insertions achieved upon the shell by modification of the epithelium at the ends of the muscles adjacent to the shell surface. Four stages in the evolution of the molluscan framework are illustrated in Figure 1. Further development of this view, its qualifications, and references are included elsewhere (STASEK, 1972). With the emergence of these ideas it became apparent that the region lying immediately adjacent to the edges of the cuticle, the future mantle margin, required special phylogenetic consideration. The present paper is addressed to that topic,

COMPARATIVE MORPHOLOGY AND INFERRED EVOLUTION OF THE MANTLE MARGIN

Synopsis: As retrospectively inferred from conditions in the 7 extant classes, the major stages in the evolution of the mantle margin were probably as follows. The initial cuticle of the predecessors was added to peripherally and in thickness as growth took place (Figure 1B, c). Spicules of calcium carbonate may have been laid down in the cuticle at intermediate stages of evolution, but later deposition of calcareous layers formed a shell and lifted the original cuticle above the secretory epithelium (Figure 1D, p). During this transition the sites of production of the now thin uncalcified portion (periostracum) became limited to a submarginal zone around the periphery of the shell. This zone was probably sunken into a shallow trough, the incipient periostracal groove (Figures 1C, 1D, pg). Surrounding the edge of the zone of periostracal secretion there extended a retractible ring of tissue, the mantle rim (Figure 1C, mr), with an accessory fold bearing mucous glands located submarginally on its undersurface (Figure 1C, af). The mantle rim, together with the accessory fold and the mantle immediately proximal to the periostracal groove, was the precursor of the mantle margin in all the higher classes. These events took place during Precambrian times, but descendants of various early intermediate forms and side branches are still with us.

The Subphylum Aculifera: The most significant of these intermediate forms are now placed together in a class, the wormlike Aplacophora (Subphylum Aculifera),

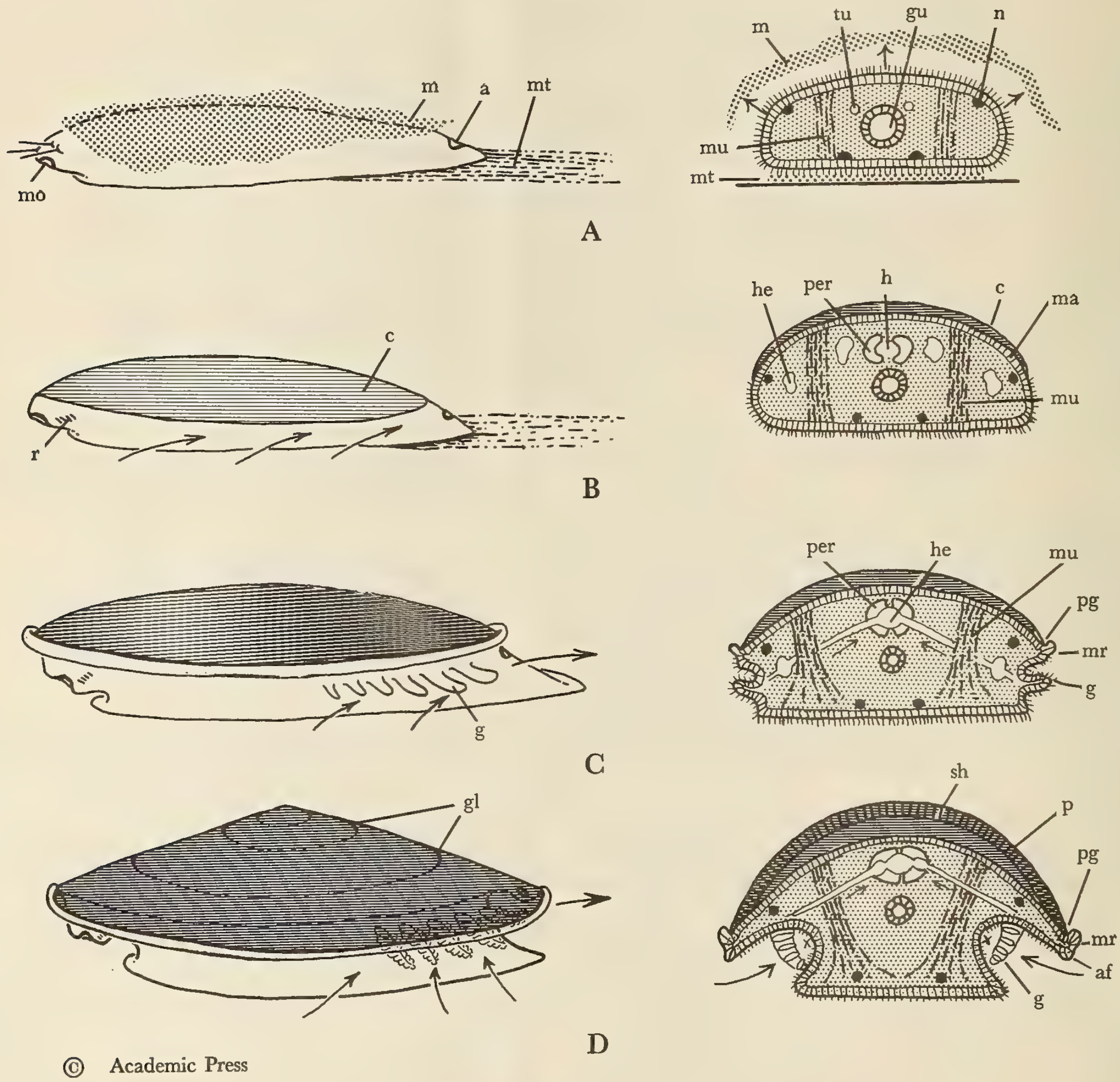


Figure 1

Four stages in the evolution of the molluscan framework from flatworm-like stock, all shown in lateral and cross-sectional aspects

A. Proposed ancestral form with complete gut and ability to secrete mucus as a protective measure and as a locomotory track.
B. Transitional stage with radula and cuticle. The cuticle is thin at the periphery where marginal growth takes place, but because the cuticle is retained throughout life, it becomes thicker in the older portions.
C. Transitional molluscan stage with an incipient mantle cavity. The cuticle arises from a shallow periostracal groove beyond which the mantle rim extends.
D. Advanced molluscan stage with calcified layers laid down under the uncalcified periostracum. The mantle rim is still simple.

a – anus; af – accessory fold of mantle associated with production of mucus; c – cuticle; g – ciliated gill; gl – growth lines; h – heart; he – unlined blood spaces; m – protective mucous coat; ma – mantle; mo – mouth; mr – mantle rim; mt – mucous track; mu – dorso-ventral muscles from which pedal muscles were derived; p – thin periostracum derived from the original cuticular layer; per – pericardium; pg – periostracal groove; r – radula; sh – shelly layers of calcified cuticle; tu – gonoducal tubules form the heart and pericardium in later stages; x – site of excurrent chamber of respiratory current; arrows in B - D indicate respiratory flow of water. From Stasek, 1972, © Academic Press, Inc.

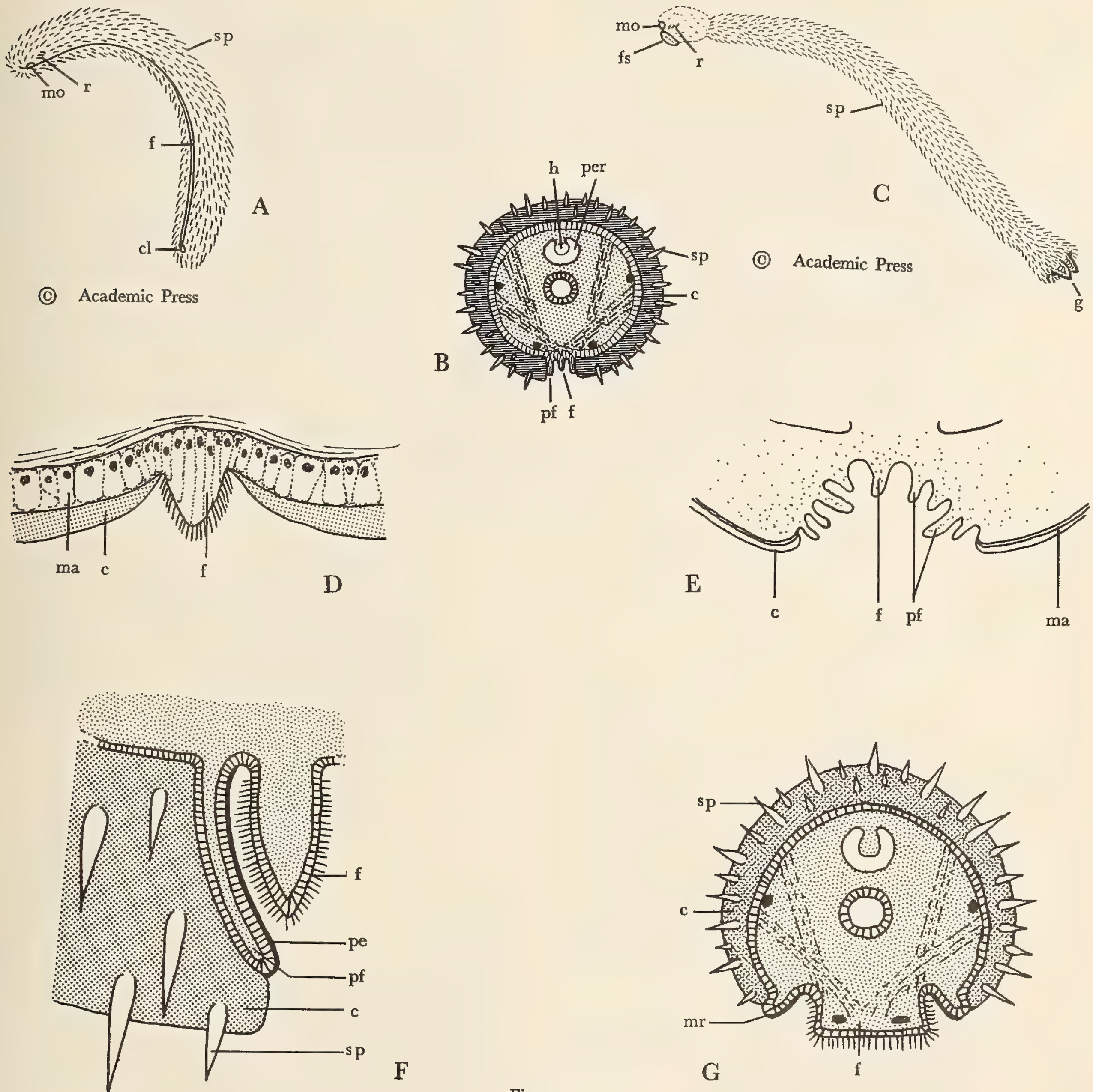


Figure 2

APLACOPHORA

A. Form with rudimentary foot and spiculous cuticle. B. Cross-section of A showing enrollment of heavy cuticle. To either side of the foot is a single pedal fold held to be homologous with the mantle rim of other mollusks. C. Form without a foot, the body being completely encircled by cuticle. D. Cross-section through foot and edges of the cuticle in a form without pedal folds. E. Cross-section through ventral region of a species with 4 pedal folds on either side of the foot. F. Cross-section of a species with one cuticular pedal fold on either side of the foot; enlarged from B. above. G. Cross-section through entire body of a hypothetical form antecedent to the more complicated enrolled Aplacophora shown in B.

c – cuticle; cl – cloaca; f – foot; fs – foot shield; g – gill; h – heart; ma – mantle; mo – mouth; mr – mantle rim; pe – pellicle; per – pericardium; pf – pedal folds; r – radula; sp – spicules. A, B, C from STASEK, 1972, © Academic Press, Inc. D, E, F suggested by HYMAN, 1967, figs. 6 and 7.

characterized not by a shell but by a spiculose cuticle that nearly or entirely encloses the body (Figures 2A, 2B, 2C). Salvini-Plawen (1969) gave class rank to each of the two body types.

In a simple instance (Figure 2D) the arrangement of the cuticular border resembles that proposed for one of the hypothetical intermediate ancestral forms (Figure 1B), except for cross-sectional proportional differences brought about by enrollment of the cuticle. Increase in diameter of the body is thought to take place by growth of the mantle above the medial edges of the cuticle (Beedham & Trueman, 1968), recalling the site of the "generative zone" of the mantle discussed below in relation to higher forms (p. 14). In these aplacophorans respiratory gas exchange probably takes place posteriorly through the unfolded walls of an enlarged cloaca (Figure 1A, cl) and through the epithelium of the foot (Leloup, 1950).

More elaborate conditions are found in those aplacophorans bearing one or more pedal folds lateral to the foot (Figures 2E, 2F, pf). In a common instance (Figure 2F) such folding gives rise to a condition reminiscent of the mantle rim of more advanced molluscan types. Folds or finger-like projections from the walls of the cloaca, as well as the pedal folds, account for respiratory gas exchange in these forms. Although any suggestion of homology, such as that made elsewhere (Stasek, 1972: 18), is strictly provisional, the anatomical similarities of these regions in aplacophorans and in the higher classes do exist, and a hypothetical form with a mantle rim is postulated as having led to more enrolled aplacophorans (Figure 2G). One may note in Figure 2F that the inner surface of the pedal fold is covered by a thin cuticular layer, the pellicle (pe). This secretion is aspiculous and its general nature differs considerably from that of the spiculose cuticle covering the body proper. The epithelia comprising either side of the pedal fold also differ: that secreting the pellicle resembles the surface of the foot, while that adjacent to the spiculose cuticle recalls the general cuticle-secreting surface of the body (Fischer-Piette & Franc, 1960: 1662).

Those Aplacophora that are completely encircled by a cuticle respire through a pair of highly folded gills resembling, and perhaps homologous with, the ctenidia of the higher mollusks (Figure 2C, g).

The Subphylum Placophora: A later, more highly evolved side branch of the Mollusca comprises the chitons, class Polyplacophora (subphylum Placophora), which have maintained the elongate body and broad foot of unrecorded ancestral forms (Figure 3A). Antecedents to this and to all succeeding classes developed the ability to regulate the deposition of calcium carbonate to form solid layers. The chitons are characterized by a shell of 8 overlapping plates, the jointing of which permits antero-posterior flexibility.

More clearly than in the proposed primitive condition, the mantle margin of the Polyplacophora is divisible into 3 regions. First there is a small fold (Figure 3B, of) medial to the periostracal groove and concerned with secretion of the shell. Second, there is the large mantle rim (Figure 3B, mr) lateral to the periostracal groove. And third, there is a swollen accessory fold bearing mucous glands on the undersurface of the mantle (Figure 3B, if; Beedham & Trueman, 1967: 221). The point to be stressed here is that the mantle rim of the ancestral mollusks was hypertrophied, forming the girdle in the Polyplacophora. This structure assures close protective contact with the substratum, except where raised to allow entrance and exit of the respiratory water currents. The surface of the girdle is exposed to the sea, but is covered by a thickened and generally spiculose cuticle (Figure 3B, c), which can be regarded as at least partially homologous with the pellicle that covers the single pedal fold of many aplacophorans.

A cuboidal or low columnar epithelium forms the general mantle surface under the shell plates (Hyman, 1967: 75). The epithelium of the girdle, in contrast, is of a high columnar nature, and the cells are peculiarly grouped into packets (Figure 3B, pa), with spaces often intervening between them. The packets of cells secrete the spicules, which project into or through the overlying

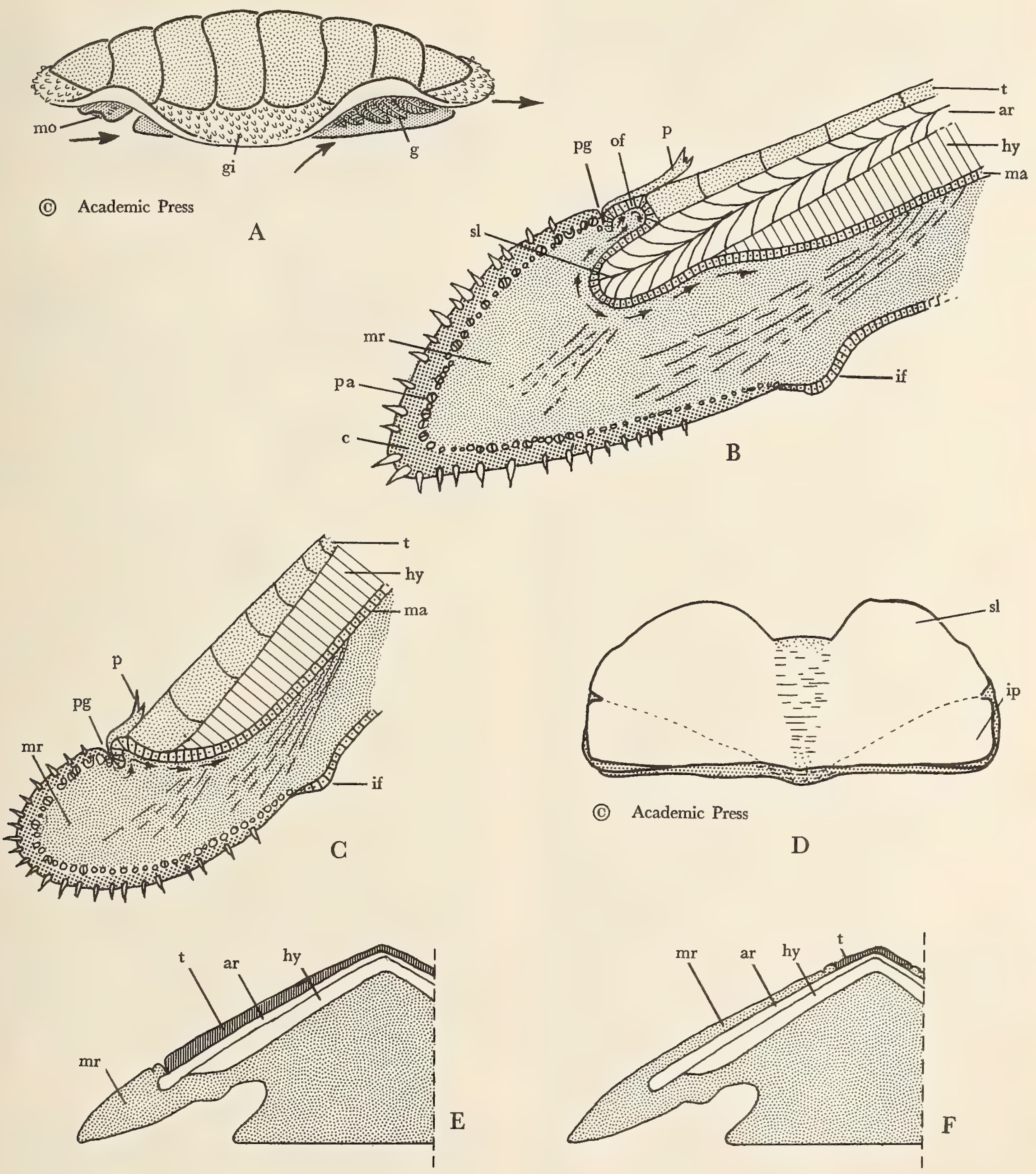
Figure 3

(on facing page →)

Polyplacophora

A. Generalized chiton from the left side showing girdle extending beyond shell plates. B. Section of shell and mantle showing enlarged mantle rim and site of periostracal groove. Small arrows suggest locations of generative zones of the mantle. C. Probable relationships of shell and mantle edge in a primitive chiton without articulamentum. D. Ventral aspect of a single valve showing structures comprising the articulamentum. E. Schematized cross-section of a chiton with extensive tegmentum. F. Schematized cross-section of a chiton with reduced tegmentum and expansive mantle covering most of the dorsal surface.

ar – articulamentum; c – cuticle; g – gill; gi – girdle; hy – hypostracum; if – inner (accessory) mantle fold; ip – insertion plate; ma – mantle; mo – mouth; mr – mantle rim (girdle); of – outer mantle fold; p – periostracum; pa – packets of epithelial cells in girdle; pg – periostracal groove; sl – sutural lamina; t – tegmentum. A and D from Stasek, 1972, © Academic Press, Inc.; B slightly modified from Stasek, 1972, based on Mutvei, 1964.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cuticular substance. The distinctly different cell types of the mantle are demarcated by the periostracal groove.

The fossil record demonstrates that there were but two calcified shell layers in the earlier polyplacophorans (Figure 3C; BERGENHAYN, 1955: 28). Differentiation of the innermost of the two primitive layers, the hypostracum (Figure 3C, hy), to form dense anterior and lateral extensions (sutural laminae and insertion plates; Figures 3B, sl; 3D, sl, ip) provided enlarged sites for muscular attachment. These extensions complicated the relationship of the shell and soft parts and comprise the third shell layer, the articulamentum (Figure 3B, ar), of modern chitons. As a specialized condition among the Acanthochitonidae and Mopaliidae, relative enlargement of the inner articulamentum and reduction of the outer tegmentum was coupled with an expansion of the girdle that may extend nearly or entirely over the entire dorsal surface of the body (Figures 3E, 3F).

The Subphylum Conchifera: The evolutionary mainstream of the phylum was determined during Precambrian times with the development of a calcified univalve shell, which was the key to the full realization of the molluscan framework as it now exists (STASEK, 1972). The most primitive univalved group to arise was the Monoplacophora, a highly diversified lower and mid-Paleozoic class with 6 or 7 living species of a single genus, *Neopilina,* having been recovered from deep water mainly in the eastern Pacific Ocean. All other higher classes of mollusks are thought to have arisen from primitive monoplacophoroids and, together with the Monoplacophora, are included in the subphylum Conchifera.

What the relationships of the mantle edge and shell may have been in the early types are unknown, but judged from the conditions in *Neopilina* and the 4 classes of mollusks considered to be descended from the Monoplacophora, there were two major kinds of association already present in the Precambrian monoplacophoroids. Transitional phylogenetic stages between the two major conditions and the ancestral condition have been illustrated in Figure 4. Of these conditions, the one typical of many gastropods (Figures 4C, 6A) and of the scaphopods (Figure 9) resembles that in the Polyplacophora and certain Aplacophora and is inferred to be primitive in that the prominent mantle rim, which may be covered by a thin cuticle (CAMPION, 1961), is not thrown into large folds and the periostracum is not tucked under the edge of the shell.

The second major association of the mantle edge and shell involved an undertucking of the periostracal groove beneath the mantle eaves (Figures 4D, 4E), a condition now characterizing *Neopilina* (Figure 5; LEMCHE & WINGSTRAND, 1959), the Bivalvia (Figure 10A; YONGE, 1957),

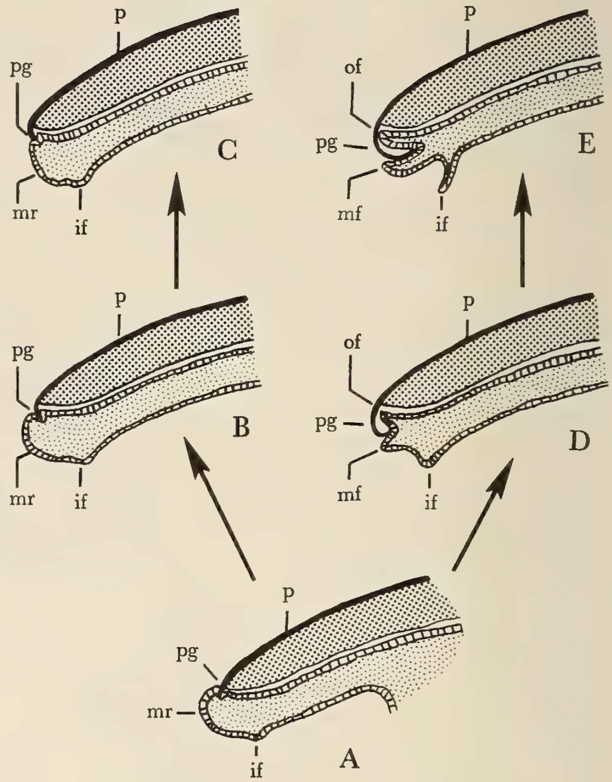


Figure 4

PHYLOGENY OF THE TWO MAJOR KINDS OF MANTLE EDGE IN THE CONCHIFERA, AS SEEN IN CROSS-SECTIONS

A. Proposed primitive type with exposed mantle rim. Retained, perhaps, in modified form by *Haliotis,* Figure 6D. B. Transitional type with mantle rim somewhat less exposed. C. Association with periostracal groove and retractible mantle rim, the primitive condition in gastropods. D. Proposed intermediate type with a three-folded mantle edge and undertucked periostracal groove. E. Association with fully formed outer mantle fold and undertucked periostracal groove, as found in *Neopilina,* bivalves, and *Nautilus.*
if – inner mantle fold; mf – middle mantle fold (mantle rim); mr – mantle rim; of – outer mantle fold; p – periostracum; pg – periostracal groove; darker areas – calcified layers of shell.

and the cephalopod *Nautilus* (Figure 11A; MUTVEI, 1964). This arrangement brought the mantle rim and periostracal groove under the protection of the overlying shell while permitting a more or less permanent association of the periostracal sheet with its secretory epithelium during retraction of the mantle edge. This reorientation probably arose polyphyletically among populations of Precambrian

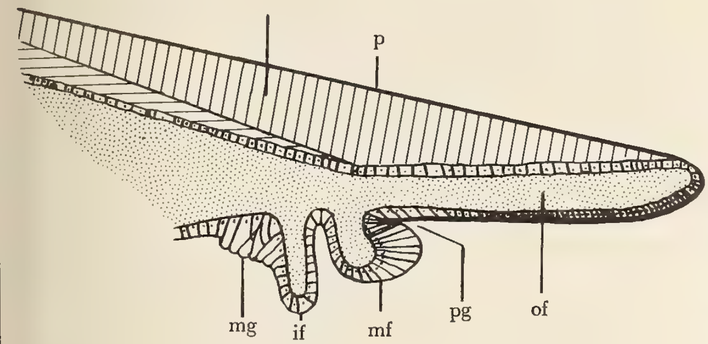


Figure 5

Neopilina

Cross-section of mantle edge showing undertucked periostracal groove and large outer mantle fold.

if – inner mantle fold; mf – middle mantle fold; mg – mucous gland; of – outer mantle fold; p – periostracum; pg – periostracal groove; sh – calcified layers of shell. Simplified from LEMCHE & WINGSTRAND, 1959, fig. 33.

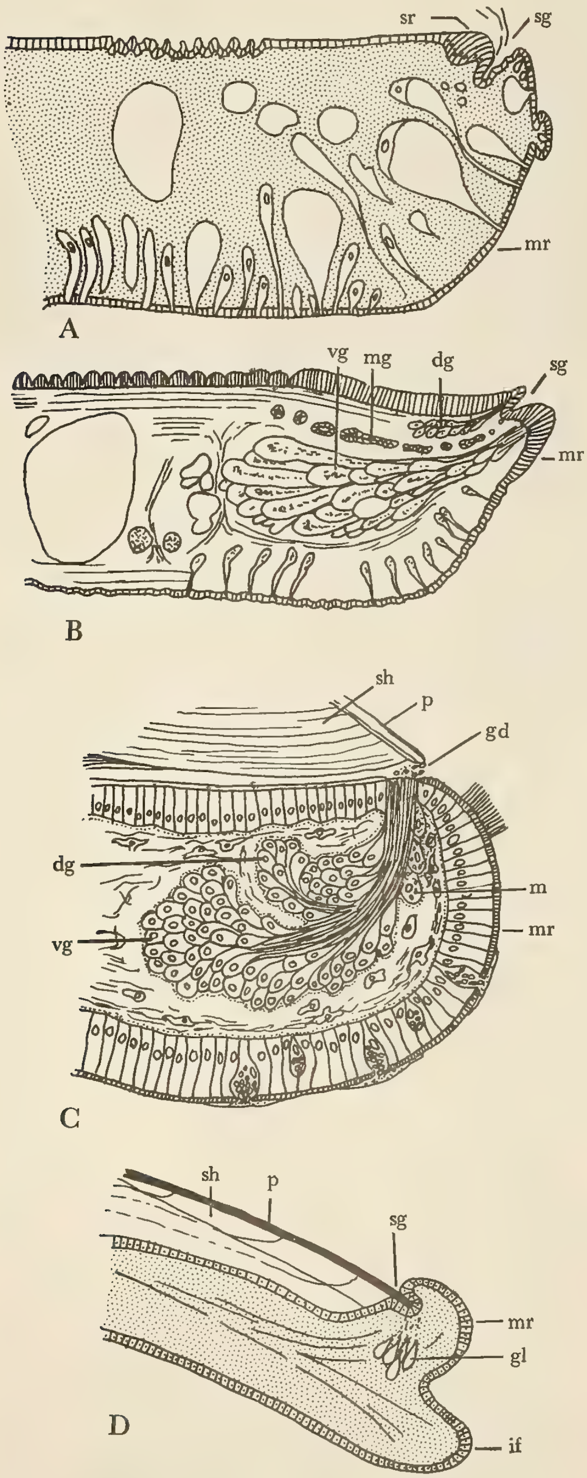
monoplacophoroids and gave rise to the state now generally regarded as typically molluscan; namely, that condition in which there is a clearly demarcated outer mantle fold (Figure 4E, of) concerned solely with secretion of the shell. The secretory ridge lying submarginally on the ventral surface of the mantle became enlarged as the inner mantle fold (Figure 4E, if), while the mantle rim, which primitively "met the environment," retained its major function of sense reception as the middle mantle fold (Figure 4E, mf).

Among gastropods, in contrast, complete protection of the mantle margin was achieved primarily through reliance upon its retraction and upon an impermanent relationship of the periostracum and its secretory epithelium. Among higher prosobranchs and many opisthobranchs a defined periostracal groove is typically lacking, and the resultant anatomical simplicity of the mantle margin could have arisen in correlation both with increased protection and with efficiency of retraction.

The Gastropoda: Among the members of this class the mantle rim is most often a simple, perhaps swollen projection in cross-section. This projection may be separated from the shell-secreting surface either by a shallow supramarginal (periostracal) groove (Figure 6A, sg), the epithelium of which may or may not be glandular in appearance; by a groove and rows of ducts issuing from large subepithelial cells (Figure 6B, vg, mg, dg); or simply by rows of ducts (Figure 6C, gd). HYMAN (1967: 189) summarized information relating to the mantle margin of prosobranchs and concluded that a supramarginal groove occurs in relatively few taxa, but is found in *Haliotis* (Figure 6D) and in the Trochidae, among others. Supramarginal grooves also occur in the primitive opisthobranch *Actaeon* and among shelled pulmonates, including the primitive genus *Siphonaria* (FRETTER & GRAHAM, 1962: 130; HYMAN, 1967: 554; JONES, 1935). This broad taxonomic distribution among primitive taxa suggests that while the presence of a defined periostracal groove is not necessarily common among the Gastropoda, it is a basic feature of the class and demarks the mantle rim from the supramarginal ridge (Figure 6A, sr). The absence of a groove is then to be regarded as a derived quality.

The supramarginal groove has been associated with the secretion of the periostracum, for example in the opisthobranch *Actaeon* (PERRIER & FISCHER, 1911) and in the pulmonate *Anguispira* (JONES, 1935). The groups of large subepithelial glands opening within or near the supramarginal groove (Figure 6B), or near the mantle margin where a groove is lacking (Figure 6C), have been interpreted as the source of periostracal material (BEVELANDER & NAKAHARA, 1970) or of shell material generally (FISHER, 1904: 36). In the limpet *Lottia* groups of glands occur at frequent intervals (FISHER, *op. cit.*). Only in very young individuals is there a continuous cordon of the glands around the mantle edge. The role of these glands was concluded to be that of shell secretion, but the evidence at present remains circumstantial, as it does in *Littorina* (BEVELANDER & NAKAHARA, *op. cit.*), for while periostracal material often can be seen emerging from the supramarginal groove where one exists, no indisputable relationship between the glandular secretions and periostracum has been demonstrated, although undoubtedly one is present.

The glandular lower surface of the mantle rim (Figures 6A, 6B, 6C) is associated with production of mucus and several other substances, including repellent or toxic secretions (FRETTER & GRAHAM, 1954; THOMPSON, 1960; EDMUNDS, 1968). Among opisthobranchs a general evolutionary trend has been towards enclosure of the shell by the reflected mantle rim and by folds of the body (Figure 7; PERRIER & FISHER, 1911). The inner mantle surface so exposed bears glands that secrete noxious material (FRETTER & GRAHAM, *op. cit.;* THOMPSON, *op. cit.*). Increasing coverage of the shell by the tissues containing these glands, and subsequent functional replacement of the shell as a means of protection, probably explains the tendency towards reduction in the relative size of the shell in this subclass.



In a few gastropods the mantle margin is molded into folds, as in *Haliotis,* where there are two (Figure 6D), and in the fissurellid prosobranchs, for example *Diodora.* where there are three (Figure 8A). While the association of the mantle rim to the periostracal groove in *Haliotis* is clearly related to the proposed primitive state (Figure 4A) and to the widespread gastropodan condition described above, that in *Diodora* is not. Rather, the orientation of the mantle edge to the shell in that genus suggests that the upper surface of the outer of the three folds (Figure 8A, of), or perhaps its distal margin, is the site of periostracal secretion. No distinct sheet of periostracum is present; certainly none emerges from the outer of the two grooves in the mantle margin. That is, the outer groove is not a periostracal groove. We conclude, therefore, that the obviously three-folded condition of the mantle margin in the Fissurellidae is not closely related to that in bivalves described below. Instead, the complexly folded mantle edge of the fissurellids represents an independent secondary folding of the mantle rim and, in *Diodora* at least, is related to a behavioral response in the presence of echinoderms (Margolin, 1964). Upon stimulation by a seastar the middle mantle fold of *Diodora* expands up over the outer shell surface, nearly covering it, while the inner mantle fold extends downward (Figures 8B, 8C). The tube feet of the seastar seem to be unable to grasp the soft mantle tissue and to be repelled by it. The body and shell of some fissurellids, such as *Megathura,* are perma-

Figure 6

(← adjacent column)

Gastropoda

Cross-section of the mantle edge.

A. *Anguispira* (Pulmonata) with swollen mantle rim and supramarginal groove without glandular ducts entering it. Variety of subepithelial gland cells is indicated on lower mantle surface. Simplified from Jones, 1935. B. *Lottia* (Archaeogastropoda) with supramarginal groove lined by three groups of subepithelial glands. Redrawn from Fisher, 1904. C. *Littorina* (Mesogastropoda) without supramarginal groove, but with large subepithelial glands associated with secretion of periostracum. Redrawn from Bevelander & Nakahara, 1970. D. *Haliotis* (Archaeogastropoda) with supramarginal groove and glands and an enlarged inner mantle fold. Simplified from Beedham & Trueman, 1967.

dg – dorsal group of gland cells; gl – gland cells; gd – ducts of subepithelial gland cells; id – inner mantle fold; m – mucous cells; mg – median group of gland cells; mr – mantle rim; p – periostracum; sh – calcified layers of shell; sg – supramarginal groove; sr – supramarginal ridge; vg – ventral group of gland cells.

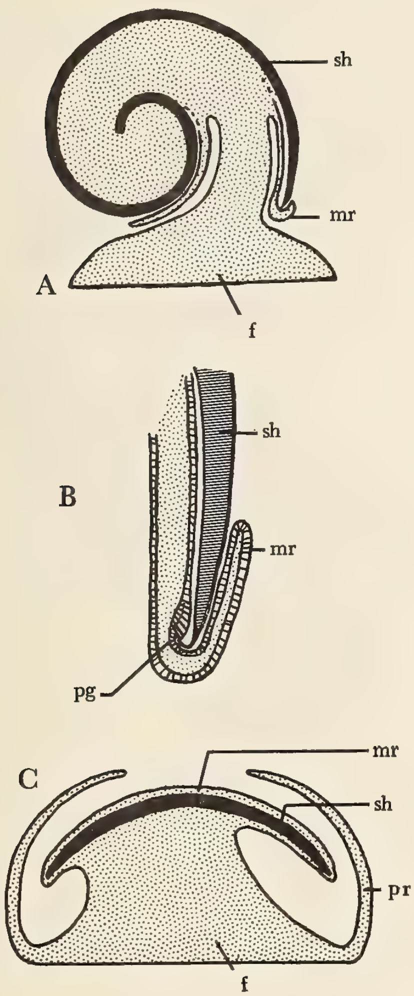


Figure 7

Enclosure of shell by the mantle in the Opisthobranchia

A. Cross-section of primitive form with large shell and mantle edge with periostracal groove. Mantle rim slightly reflected over lip of shell. Based on *Actaeon*. B. Enlarged section of mantle edge of *Actaeon*. C. Cross-section of advanced type with reduced shell enfolded by mantle rim and with parapodia extending from foot. f – foot; mr – mantle rim; pr – parapodia; sh – shell. A and B suggested by Perrier & Fischer, 1911, p. 8, fig. B, and plt. 4, fig. 8. C suggested by Lang, 1896, p. 47, fig. 56.

nently covered by overgrowth of the middle and inner mantle folds (Figures 8D, 8E; Odhner, 1932); this also is probably a defensive measure.

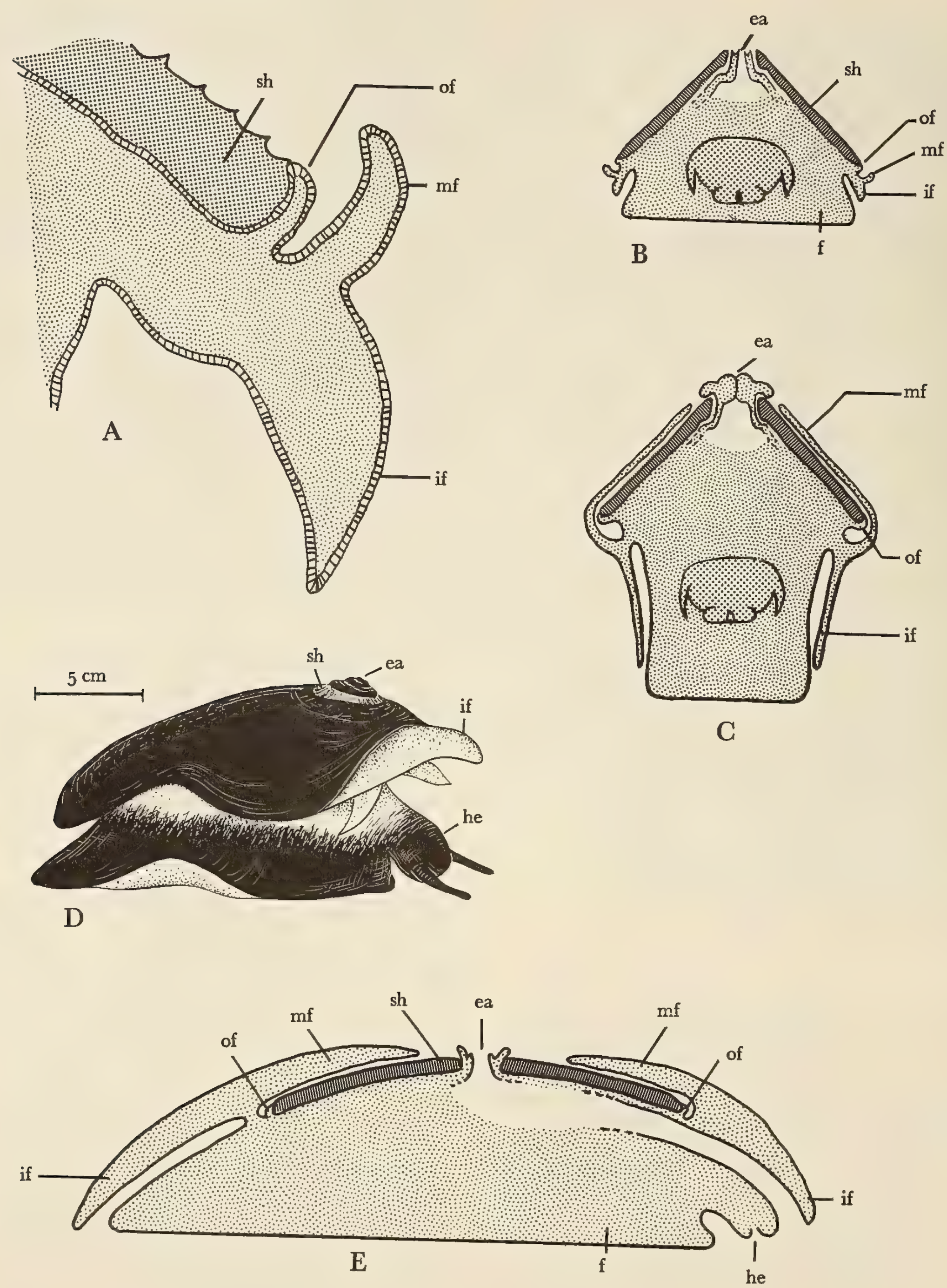
The Scaphopoda: The mantle rim at the anterior end of *Dentalium* (Figure 9A) is greatly enlarged and contains numerous flask-shaped subepithelial mucocytes on its lateral surface (Boissevain, 1904). The muscular rim is wedge-shaped in section and functions in burrowing by acting as a diaphragm around the foot, thus preventing material of the substratum from entering the anterior mantle cavity (Dinamani, 1964). Mucus, which is released in copious amounts upon the outer surface of the mantle rim, may act as a protective lubricant and has been observed by one of us (W. McW.) to bind particles of the substratum together.

The mantle edge lining the smaller, posterior opening of the shell is characterized by a modified epithelium and musculature and is termed the pavilion (Lacaze-Duthiers, 1856-1857). Flask-shaped subepithelial mucocytes resembling those of the anterior rim are present, but they are smaller and are associated with the medial, rather than the lateral surface of the mantle edge (Figure 9B). The lateral surface of the posterior mantle edge is responsible for the secretion of fragile calcareous, secondary extensions of the shell in many species (Figures 9B, 9C, ce), and may also be involved in resorptive truncation of the shell apex.

The cuboidal epithelium on either side of the shallow supramarginal groove (Figures 9A, 9B, sg) grades into a membrane so thin at the base of the groove that cells cannot be distinguished by light microscopy. Because there is no periostracum in scaphopods, the absence of secretory indications in the supramarginal groove is to be expected.

The Bivalvia: The Bivalvia have provided most of the existing information on the molluscan mantle and shell in terms of anatomy (Yonge, 1957), structure (Grégoire, 1972), mineralogy (Kennedy *et al.*, 1969), calcification (Wilbur, 1972), and shell regeneration (Beedham, 1965; Saleuddin, 1967). Because of their early prominence in investigations, the Bivalvia have supplied bases for comparisons and expectations in all of the other classes. The terms used to describe the relative conditions of the mantle margin throughout the phylum reflect this. For example, the zone of shell secretion just medial to the periostracal groove in chitons (Figure 3B, of) and gastropods (Figure 6A, sr) has been described as a reduced outer mantle fold. That this region never was prominent in either of these classes is much more likely.

Among bivalves the mantle edge is universally comprised of three basic folds (Figure 10A; Yonge, 1957), being found in members of all three subclasses: Protobranchia (Stempell, 1898), Lamellibranchia (Drew,



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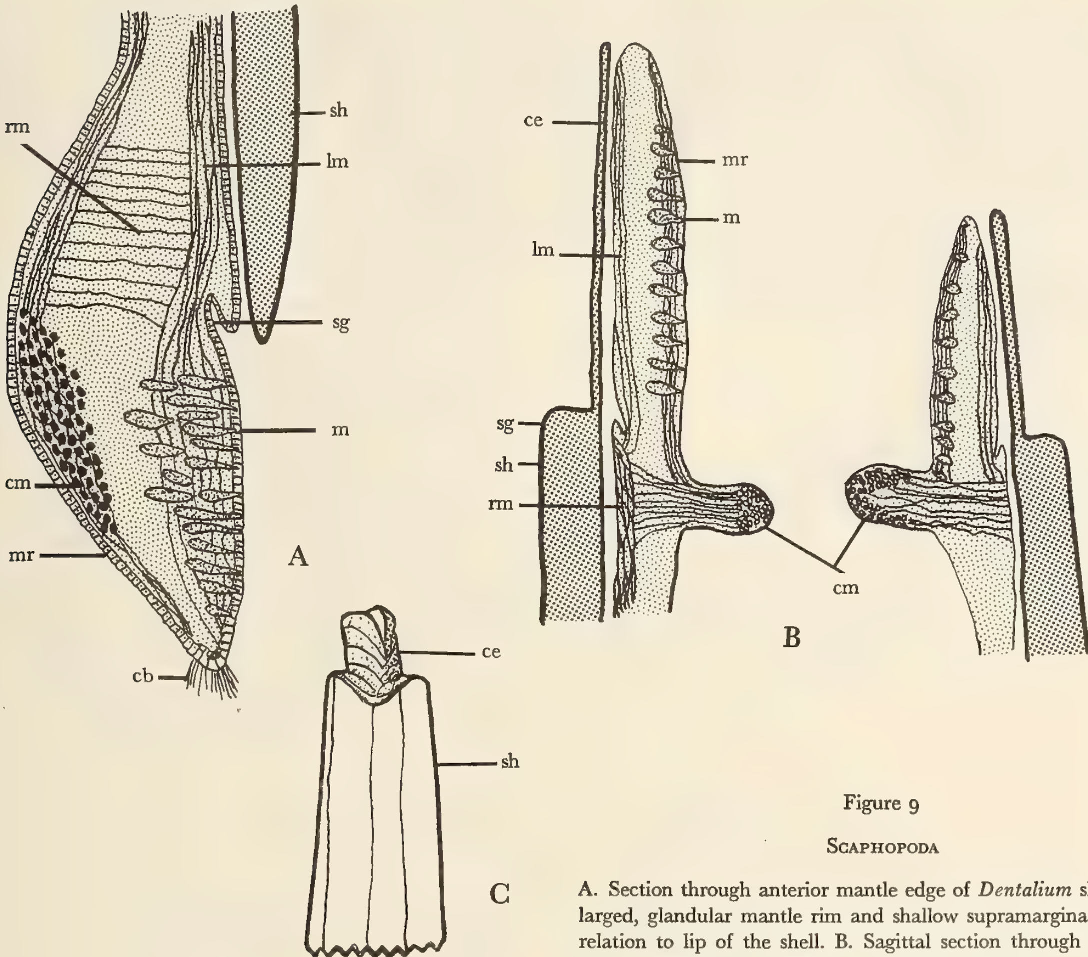


Figure 9

SCAPHOPODA

A. Section through anterior mantle edge of *Dentalium* showing enlarged, glandular mantle rim and shallow supramarginal groove in relation to lip of the shell. B. Sagittal section through dorsal and ventral surfaces of pavilion showing relationships to end of shell with its secondary extension. C. Posterior end of shell showing secondary extension with slit.

cb – ciliary band; ce – secondary calcareous extension at posterior end of shell; cm – circular muscles; lm – longitudinal muscles; m – mucocytes; mr – mantle rim; rm – radial muscles; sg – supramarginal groove; sh – shell.

Figure 8

(← on facing page)

FISSURELLIDAE

A. Cross-section of mantle edge of *Diodora* showing three folds. Simplified from FRETTER & GRAHAM, 1962, fig. 80. B. Cross-section of entire *Diodora* showing relationships of shell and mantle in undisturbed state. Redrawn from MARGOLIN, 1964. C. Relationships following stimulation by seastar. Note expanded middle fold covering the shell, and inner fold, which is extended ventrally over heightened body. Redrawn from MARGOLIN, 1964. D. *Megathura* as seen from the right side, with anterior margin of inner fold raised revealing the gills in the mantle cavity. Adjacent to the exhalant aperture a small portion of the shell is exposed. Drawn from life by Emily Reid and included here by courtesy of Dr. R. Stohler. E. Longitudinal section of *Megathura* showing relationships of the permanently expanded fleshy inner and middle mantle folds covering the shell. Suggested by ODHNER, 1932, fig. 21.

ea – exhalant aperture; f – foot; he – head; if – inner mantle fold; mf – middle mantle fold; of – outer mantle fold; sh – shell.

1906; SULLIVAN, 1961; GALTSOFF, 1964; SALEUDDIN, 1967), and Septibranchia (personal observations, C. R. S.). In all of these the depression between outer and middle folds forms a periostracal groove from which the periostracum emerges, folds back around the edge of the calcareous portion of the shell, and lies appressed to its outer surface (Figure 10A). Although it is the cells of the groove and of the medial surface of the outer fold that are concerned with secretion of the layered periostracum

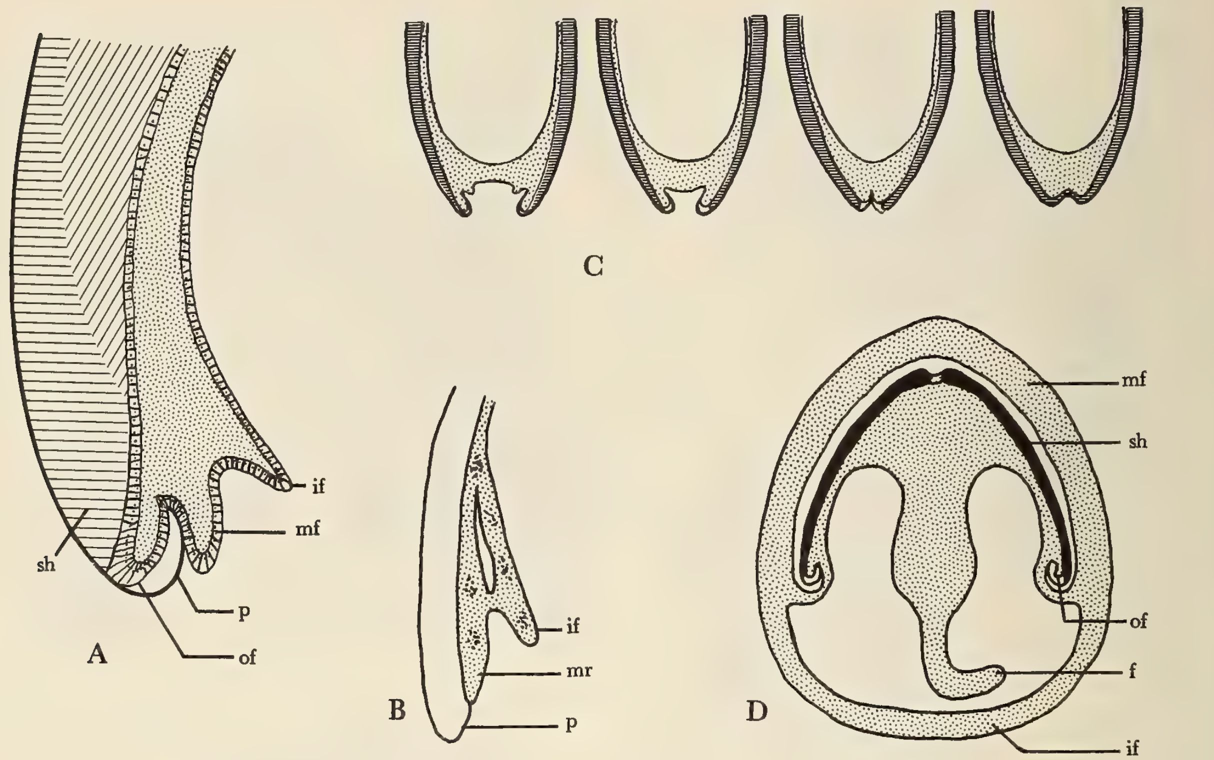


Figure 10

Bivalvia

A. Generalized cross-section of mantle edge showing three-folded nature and undertucked periostracum. Note that periostracum is adherent to lateral surface of middle mantle fold. B. Cross-section of mantle edge of metamorphosing *Venerupis* showing simple mantle rim, the periostracum arising from its margin. Simplified from Quayle, 1952, fig. 3 A. C. Various degrees of cross fusion of left and right sides of ventral mantle edges; in order, inner folds only, inner folds with medial surface of middle folds, inner and middle folds, and all three folds including the medial surfaces of outer mantle folds. From Yonge, 1957, fig. 5. D. Cross-section of a galeommatid bivalve with reduced shell completely enfolded by the middle mantle fold. Suggested by Popham, 1939, figs. 11 and 16. f – foot; if – inner mantle fold; mf – middle mantle fold; mr – mantle rim; of – outer mantle fold; p – periostracum; sh – shell.

(Bevelander & Nakahara, 1967), this material, once it is tanned, is adherent to the lateral surface of the middle fold (Figure 10A, mf). As recently as 1965, there were those who held to an older view that the latter site was responsible for elaboration of periostracal substance, at least in certain bivalves (Saleuddin, 1965: 238). A gradual distal thickening of the periostracal layer facing away from the middle fold, as indicated in Saleuddin's figure 3, suggests that this view is technically erroneous. This does not eliminate the possibility that the middle fold plays some subtle role in shell secretion (Hillman, 1969: 424).

The outer mantle fold and the deepened periostracal groove arise in bivalves from a much simpler condition during metamorphosis of the larva (Figure 10B; Meisenheimer, 1900, figures 112, 113; Drew, 1901; Quayle, 1952; Creek, 1960; Allen, 1961; Ansell, 1962). The periostracum is initially attached along the very edge of the mantle, which does not bear evidence of secretory activity or even of cell membranes between its nuclei in many instances. A submarginal fold, the future inner mantle fold, may or may not be present (*e.g.*, *Venerupis* and *Nucula*, respectively). With further development, the more distal fold splits, resulting in two ridges, now the

outer and middle mantle folds, and the periostracum emerges from the groove between them. The apparent splitting of the originally undivided mantle edge probably takes place through differential growth, although data are lacking.

Apposition of left and right sides of the mantle in this laterally compressed group has led to various degrees of fusion (Figure 10C; YONGE, 1957), and in relation to the evolution of burrowing habits, to the formation of siphons (STANLEY, 1968). In such instances the three-folded nature of the mantle edge is obscured. Rarely, a fourth fold makes its appearance, as in the venerid clam *Mercenaria* (HILLMAN & SHUSTER, 1966). Histological observations suggest that the fourth fold is an elaboration combining portions of the medial surface of the third fold and of the general inner surface of the mantle surface immediately proximal to the third fold.

As in gastropods, the various regions of the bivalve mantle margin are associated with several kinds of epithelial and subepithelial secretory cells, generally mucocytes (SULLIVAN, 1961; HILLMAN, 1968), as well as others that are probably associated with calcification (HILLMAN, *op. cit.*) or with substances concerned with the tanning of periostracal material (HILLMAN, 1961).

The mantle has become highly modified in many bivalves. In relation to what is presumed to be the original function of sense reception, the middle mantle fold may bear eyes, either simple ones, as in *Cardium* (ROCHE, 1925) and *Tridacna* (STASEK, 1966), or complex ones, as in the Pectinidae (DAKIN, 1928). Sensory tentacles also represent elaborations of the mantle rim, as in *Lima*, which, in addition, may be related to protection in that the tentacles are sticky and autotomous (GILMOUR, 1967).

In relation to nutrition, it is the middle mantle fold of the siphonal regions of the giant clams that is greatly enlarged (YONGE, 1953). Symbiotic dinoflagellates housed there have been shown to release significant amounts of glycerol during metabolism, a substance that may be utilized by the bivalves as a source of energy in nutrient-poor tropical waters (MUSCATINE, 1967).

In certain genera of the families Galeommatidae and Montacutidae the mantle rim is reflected back over the shell, making it partially or entirely internal (Figure 10D; POPHAM, 1939; JUDD, 1971). Reduction of the relative size of the shell is a corollary trend, suggesting that, as

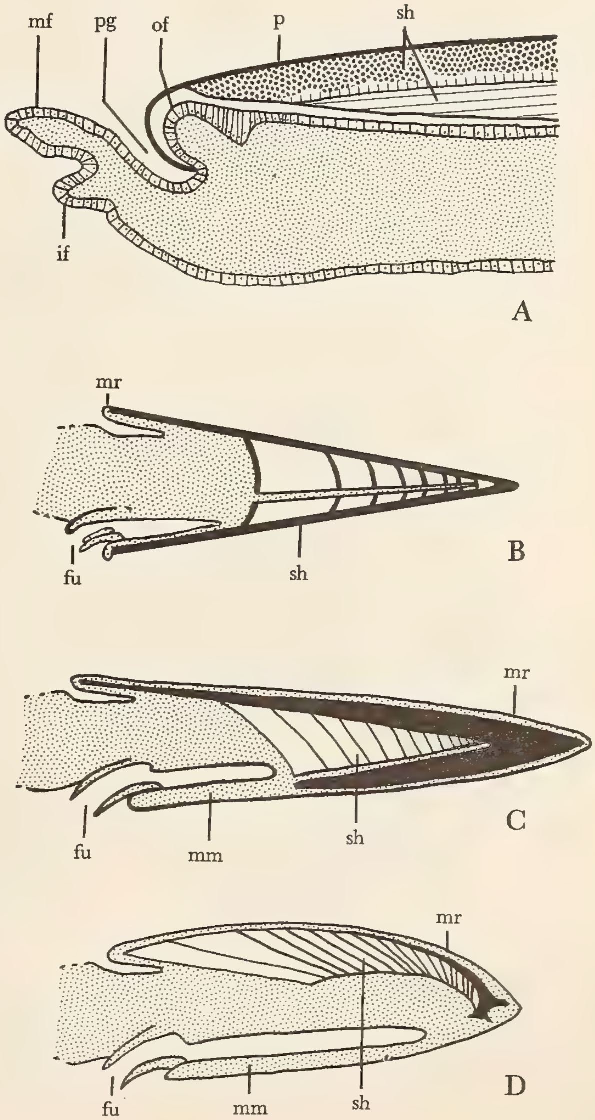


Figure 11

(adjacent column →)

CEPHALOPODA

A. Cross-section of mantle edge of *Nautilus* showing its three-folded nature and undertucked periostracum. B. Longitudinal section of stylized primitive nautiloid with mantle rim that terminates at lip of large, chambered shell. C. Probable relationships of extinct bellerophont showing mantle rim that has enfolded the shell, which is partially reduced ventrally in correlation with muscularization of the mantle. Secondary calcareous deposits (black) form a heavy rostrum. D. *Sepia*, the cuttlefish, showing reduced shell and rostrum (black) and muscular mantle, the rim of which covers the shell.
fu – funnel (foot); if – inner mantle fold; mf – middle mantle fold; mm – muscularized mantle; mr – mantle rim; of – outer mantle fold; p – periostracum; pg – periostracal groove; sh – shell. Trends in B, C, and D suggested by NAEF, 1928, figs. 43 and 59, and MOORE *et al.*, 1952, p. 344.

in the opisthobranch gastropods, an alternative defensive mechanism may be involved, although POPHAM (*op. cit.*: 82) related it to the commensal mode of life of these bivalves.

The inner fold generally is associated with controlling the flow of water into the mantle cavity (YONGE, 1957) and forms the muscular velum (Figure 10A, if). In relation to boring in calcareous rocks, the inner fold of the mytilid *Lithophaga* secretes an acid that etches the substratum (YONGE, 1955; HODGKIN, 1962).

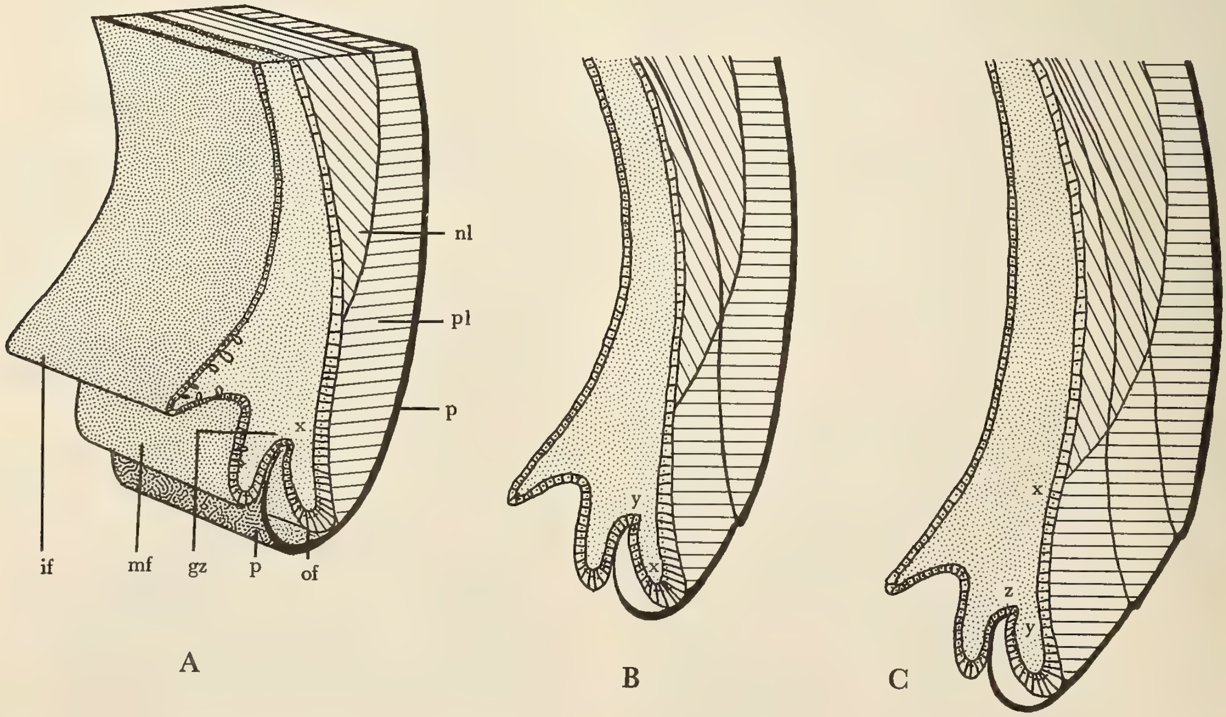
The Cephalopoda: Among living cephalopods, *Nautilus* alone bears an external shell, a mantle edge with an undertucked periostracal groove, and three fairly distinct mantle folds (Figure 11A; MUTVEI, 1964). Thus, in *Nautilus*, and probably in most extinct nautiloids (Figure 11B), the mantle rim terminates at the lip of the shell. The shells of all other existing cephalopods have been engulfed by overgrowth of the mantle rim (Figures 11C, 11D, mr; NAEF, 1928). Reduction of the shell is again a corollary, in this instance related to increased lightening and streamlining of the body in the cuttlefish and squids, and to pumping of the muscular mantle (Figures 11C, 11D, mm), which supplies the locomotory jet force in these pelagic mollusks (TRUEMAN & PACKARD, 1968). Attachments of the mantle edge to a large shell, as in the nautiloids, would not foster this mode of propulsion.

Figure 12

GENERATIVE ZONE OF THE MANTLE

A. Stereodiagram of mantle edge of a bivalve showing relationships of the 3 folds, periostracum, and shell layers. Cells "x" arising from depths of the outer groove produce periostracal material. B. Cross-section of same mantle edge at later growth stage (note growth line). Cells "x" have been shifted to a position at the margin of outer mantle fold by formation of cells "y". Secretory products of cells "x"has altered from periostracum to crystals of calcium carbonate in an organic matrix. That portion of periostracal sheet manufactured by cells "x" is now located at the edge of the calcified layers. C. A still later growth stage (note second growth line). Cells "x" further displaced and now secrete nacreous material. Cells "y" have been displaced by new cells "z". Cells "z" secrete periostracum, which has maintained physical continuity throughout the growth stages.

gz – generative zone of mantle; if – inner mantle fold; mf – middle mantle fold; of – outer mantle fold; p – periostracum; pl – prismatic shell layer; nl – nacreous shell layer. Suggested by MUTVEI, 1964, fig. 9.



A thin cuticle covers the general epithelium of *Octopus* (GUÉRIN, 1908) and of the cuttlefish (FIORONI, 1963) and is probably a feature of the skin of other cephalopods as well.

THE GENERATIVE ZONE OF THE MANTLE

A ring of periostracum-secreting cells separates the mantle rim from the remaining shell-secreting surface of the mantle. In those groups with an undertucked periostracal groove the sheet of periostracum arises in the depths of the groove and bends around the edge of the shell to become appressed to its outer surface (Figure 12A). The situation is not difficult to understand if it is regarded as static, but the fact of peripheral growth confuses the issue. The way in which the periostracum is shifted in position from its site of origin to the outer shell surface, yet retains its association with the periostracal groove during enlargement of the mantle, is far from clear. Present evidence indicates the following course of events (MUTVEI, 1964), which probably applies to all the Mollusca.

Cells at the bottom of the periostracal groove, or possibly first arising below the epithelium (DUNACHIE, 1963), are inferred to comprise a generative zone of the entire mantle. By successive divisions the cells of the generative zone push those produced earlier out onto the medial surface of the outer mantle fold, as illustrated in Figures 12A, 12B. The periostracal sheet produced by those cells is simultaneously moved or "unrolled" outwardly from the groove. During their passage, the cells enlarge and continue to have periostracal material as their secretory product. The requisite cell divisions of this process appear to be amitotic, for mitotic figures have yet to be observed (DUNACHIE, *op. cit.*), even in very young individuals. As stated by CATHER (1967) with reference to the snail *Ilyanassa,* the cells of the mantle of metamorphosing individuals become flat and show no morphological signs of activity. The mantle edge appears to grow through incorporation of surrounding ectodermal cells, as well as through proliferation. Division figures seen in the shell gland of earlier stages never occur in differentiated mantle cells of *Ilyanassa.* That mitotic rhythms may take place was suggested by the work of HILLMAN (1963), who demonstrated division figures in regenerating mantle epithelium of the oyster *Crassostrea virginica.*

As the cells are displaced towards the edge of the outer mantle fold their histological appearance alters in one of several ways, and their secretory product changes from periostracum to calcium carbonate and an organic matrix upon which the calcium is deposited in crystalline (prismatic) form. The epithelial cells continue their movement and now comprise part of the outer surface of the mantle (Figures 12B, 12C). Their histological nature undergoes further changes, generally becoming lower. When the cells reach the outer submarginal region of the mantle (point "x" in Figure 12C), the crystalline material they secrete shifts from prismatic to nacreous.

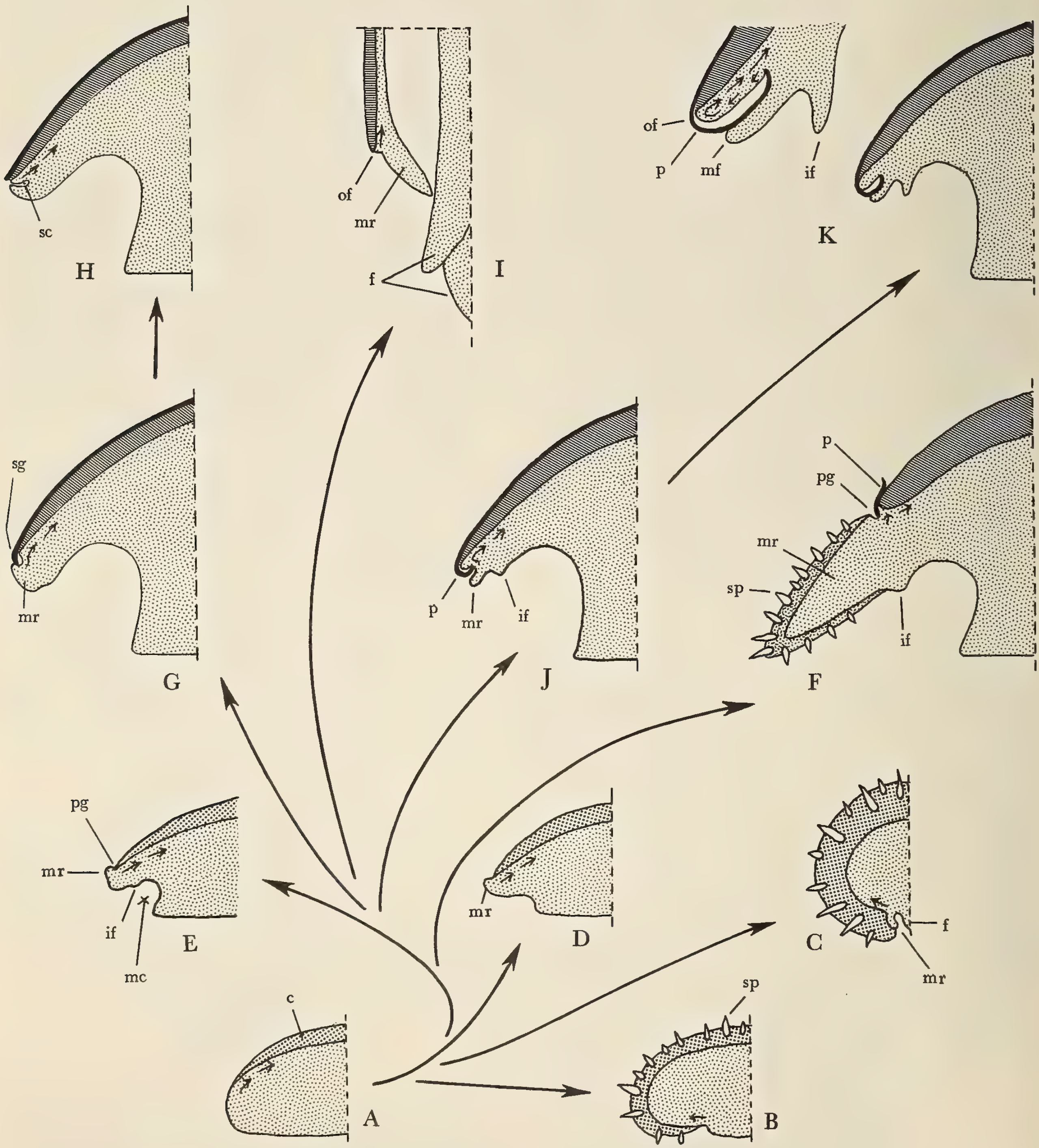
In summary, each cell originating in the generative zone of the periostracal groove is destined to be displaced by others emerging behind it and to pass over the lip of the outer mantle fold, undergoing an orderly sequence of histological and secretory modifications as it does so. The complexly layered shell is the product of this emigration with the various layers and sublayers being laid down in temporal sequence from outer to inner. Because of the unusual conformities of their valves, additional generative regions must somehow exist at the anterior edges of the sutural laminae of chitons (Figure 3B, sl; BERGENHAYN, 1930; BEEDHAM & TRUEMAN, 1967).

The entirely circumstantial evidence for the existence of a generative zone has been summarized by MUTVEI (1964). Transitional cell types between distinctive epithelial regions of the mantle edge of the gastropod *Berthelinia* (KAWAGUTI & IKEMOTO, 1962) and the bivalves *Fabulina* and *Musculus* (KAWAGUTI, 1963) provide some histological evidence that in life all the cells of the mantle experience emigration from a region of proliferation and undergo gradual alterations of form as their position is shifted. A sequence of secretory and form changes is known to occur in cells located in regenerating mantle tissue of bivalves (KAWAGUTI, *op. cit.*; BEEDHAM, 1965) and of the snail *Helix* (SALEUDDIN, 1970), although these cells in *Helix* never come to resemble those at the mantle edge.

More secure evidence for the existence of a generative zone has been found in brachiopods (WILLIAMS, 1969), so that the process has an analog elsewhere among shelled organisms. The generative zone in that phylum lies medial to the actual edge of the periostracal sheet on the undersurface of the mantle; the initial product of the cells is a mucoid substance, probably a mucopolysaccharide (WILLIAMS, 1968). The secretion of periostracum takes place under the protective cover of this material.

CONCLUSIONS

The site of periostracal secretion has been regarded in this paper as a basic landmark for the determination of homologous regions of the mantle edge throughout the Mollusca. While they, themselves, were not antecedent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to the higher classes, the variety of conditions exhibited by living Aplacophora suggests that there was a multiplicity of associations at the edge of the cuticle among the molluscan precursors (Figures 13A to 13D). The stocks characterized by only one of these associations, that in which a mantle rim and periostracal groove were developed, were successful in giving rise to advanced forms. Figure 13 depicts our interpretation of the phylogeny of the mantle edge from such an ancestor (Figure 13D). The primitive condition of the mantle margin in the early Mollusca is concluded to have been much simpler than hitherto believed. Instead of three folds, only one, the mantle rim, was at first distinct and became manifest even in a few aplacophorans (Figure 13C), but was hypertrophied as the cuticularized girdle in the chitons (Figure 13F). Cuticularization of the mantle rim also became evident in some aplacophorans, in certain gastropods, and perhaps in all cephalopods.

Among conchiferan mollusks, the basic conformities of the earlier condition have been retained by scaphopods (Figure 13I) and by most of the more primitive gastropods (Figure 13G). Active withdrawal of a simple mantle

Figure 13

(← on facing page)

Phylogeny of the mantle edge in the Mollusca, as seen in cross-sections.

A. Cuticularized turbellariform ancestor. B. Proposed spiculose intermediate type related to the Aplacophora without pedal folds or mantle rim (Figure 2D). C. Aplacophora with single pedal fold (mantle rim) and narrow foot. D. Proposed ancestral condition in which a mantle rim projects beyond the margin of the cuticle. An incipient periostracal groove is present. E. A more advanced type with deeper mantle cavity and possibly lacking calcified shell layers. F. Polyplacophora with enlarged, cuticularized, and spiculose mantle rim (girdle). Calcified layers laid down under transient periostracum. G. Primitive condition in gastropods with projecting mantle rim and a supramarginal groove. H. Advanced condition in gastropods without supramarginal groove. I. Scaphopoda with enlarged mantle rim acting as a diaphragm around the foot. J. Proposed intermediate form with partially undertucked periostracal groove and enlarged inner mantle fold. K. Generalized cross-section and enlargement of the probably convergent condition in *Neopilina,* bivalves and *Nautilus,* all with well formed outer mantle fold and undertucked periostracal groove. c – cuticle; f – foot; if – inner mantle fold; mc – mantle cavity; mr – mantle rim; of – outer mantle fold; p – periostracum; pg – periostracal groove; sc – subepithelial secretory cells; sg – supramarginal groove; sp – spicules; calcified layers of shell are darker, uncalcified cuticle lighter. Small arrows suggest probable directions taken by cells from generative zones of the mantle.

margin from the aperture of the shell, as in advanced prosobranchs (Figure 13H), or undertucking of the periostracal groove with concomitant increase in the complexity of the mantle margin combined with its withdrawal, as in bivalves (Figures 13J, 13K), represent alternative means of lending increased protection to the mantle edge.

In all likelihood, the mantle-shell associations that appeared in the phylum arose through simple variations of differential growth, as described for bivalves (p. 12) and as suggested in Figure 4. Variation in overall shell form achieved through differential growth about the periphery of the mantle, and alterations in the direction of this growth, are related aspects to be taken into account when considering success and diversity of the molluscan framework. Analyses of these geometrical attributes of shell growth have been meaningfully approached by Raup (1961, 1962, 1966, 1967), by Raup & Chamberlain (1967), and by Carter (1967). The adaptive significance of shell form has hardly been touched upon, however. The publications by Stanley (1970, 1972) and by Thayer (1972) on bivalves represent excellent and fruitful approaches to this topic.

The mantle, especially the mantle rim, has folded back over the shell in several taxa, including representatives of the Polyplacophora (Acanthochitonidae), the Gastropoda (Fissurellidae, Opisthobranchia), the Bivalvia (Galeommatidae, Montacutidae), and the Cephalopoda (Coleoidea). Generally, there is corresponding reduction of the shell in these forms. The adaptive significance of enfoldment has been fairly treated in the literature only for the gastropods and cephalopods.

The "unrolling" of the shell-secreting epithelium from a generative zone of the mantle and the temporal sequence of secretory activity undergone by the cells as they emigrate out of the periostracal groove, or its equivalent where a groove is absent, are inferred to have been related to the early selection of the successful molluscan stem-groups in that these processes led not only to the evolution of an organized calcified shell that grew by peripheral accretion, but provided a mechanism that permitted evolutionary size increases while lending a means of protection to the soft parts regardless of their size. Trends towards larger size from relatively tiny ancestral forms characterize all of the higher molluscan classes (Stasek, 1972: 11). The mechanism underlying accretionary shell growth, combined with the tendencies towards larger size fostered by this mechanism, were factors of paramount importance in severing the ties with the original turbellariform groundplan and in establishing the Mollusca as a significant phylum.

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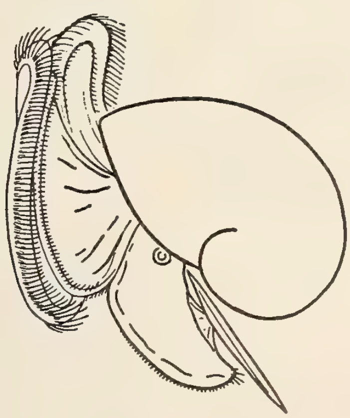

A New Genus and Two New Species of Land Snails from the Lau Archipelago of Fiji

BY

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(3 Plates; 6 Text figures)

INTRODUCTION

SEVERAL COLLECTIONS OF LAND MOLLUSKS were made on some islands of the Lau Archipelago of Fiji by Harry S. Ladd in the early 1930's and by members of the Henry G. Lapham Expedition from the Bernice P. Bishop Museum in 1938. Despite this, many islands never have been sampled for mollusks. On others, only fragmentary collections were made during a few hours. Despite the limited material available, it is obvious that Lau is a major center of Pacific Island land snail diversity.

In late 1970, Mr. Laurie Price of Kaitaia, New Zealand, collected on several islands for Field Museum of Natural History. Among the many mollusks obtained are the two very remarkable species of endodontid land snails described below. ***Priceconcha tuvuthaensis*** is a new genus and species from Tuvutha or Tuvuca Island, located approximately at 178°48'W and 17°40'S, and *Thaumatodon **spirrhymatum*** is an extraordinary new species from Thithia or Cicia Island, located approximately at 179°20'W and 17°45'S.

A monograph of the Pacific Island Endodontidae (SOLEM, in press) was completed prior to receipt of this material. Rather than undertake extensive renumbering of charts, tables, and illustrations, it was decided to publish on these separately and insert only cross-references into the major work. Data concerning the criteria used to weigh characters and the bases for classification decisions are included in the main report and are not repeated here.

ACKNOWLEDGMENTS

Support for this work was received from NSF Grant GB-6779. The excellent line drawings were prepared by Carole W. Christman. Scanning Electron Microscope photographs were made during the course of cooperative research work with the American Dental Association Research Institute. I am deeply indebted to George Najarian and John Lenke of their Electron Optics Laboratory for assistance, to Fred Huysmans of Field Museum of Natural History for preparing the photographic prints, and to Mrs. Dorothy Karall for mounting and lettering the several figures.

SYSTEMATIC REVIEW

GASTROPODA

SIGMURETHRA

ENDODONTIDAE

Priceconcha Solem, gen. nov.

Endodontidae in which the major radial sculpture has been lost, microsculpture absent on spire and reduced to barely visible remnants on the last whorls. Shell larger than average, with greatly increased whorl count, averaging more than $7\frac{3}{8}$ whorls in adults. Spire and apex strongly and almost evenly elevated, slightly rounded above, last whorl not descending, H/D ratio averaging about 0.555. Umbilicus broadly "V"-shaped, regularly decoiling, last whorl not decoiling more rapidly, contained about 2.90 times in the diameter, margins sharply rounded. A strong, thread-like keel and prominent supraperipheral sulcus present. Parietal wall with 5 barriers and 10 or 11 accessory traces extending more than a full whorl posteriorly. Columellar lamellae 2, with 2 accessory traces. Palatal wall with 4 subperipheral and

1 supraperipheral barriers, plus 4 or 5 accessory lamellar traces. All major barriers with fine beading above. Radula typical endodontid, with tricuspid central, bicuspid laterals, marginals tricuspid with split ectocones. Genitalia greatly elongated, particularly in free oviduct and vas deferens area, basic structures as in *Thaumatodon*.

Type species: ***Priceconcha tuvuthaensis*** Solem, spec. nov.

Generic separation is based on the extreme conchological modifications seen in ***Priceconcha tuvuthaensis*** compared with the average endodontid pattern and the range of variation present in *Thaumatodon*. The great increase in whorl count, to more than $7\frac{3}{8}$ compared with a median $5\frac{1}{2}$+ for the Endodontidae and mean $5\frac{1}{4}$– in *Thaumatodon*, striking reduction in shell sculpture, altered shape and coiling pattern, plus the extreme elongation of the apertural barriers are major changes. Conchologically, the most similar appearing genus is the Society Island *Nesodiscus*, particularly such species as *N. fabrefactus* (Pease, 1864) and *N. fictus* (Pease, 1864). These show the same pattern of increased whorl count and reduced sculpture, but are much larger in size, have greatly reduced apertural barriers, and lack the development of an epiphallus and shift in spermathecal insertion seen in ***Priceconcha***. The differences between *Thaumatodon* and ***Priceconcha*** are of the same order of magnitude as the differences between *Nesodiscus* and its currently unnamed progenitor, the conchological equivalent of *Thaumatodon*.

In general appearance, the shell of ***Priceconcha*** seems to be a small, colorless trochomorphid. Only the remnant sculpture, visible at 96X or above, and the presence of beaded apertural barriers, show that it is an endodontid.

Great pleasure is taken in dedicating this genus to Mr. Laurie Price from Kaitaia, New Zealand. A Field Associate at Field Museum of Natural History and long-time collaborator in my work on Pacific Basin land mollusks, Mr. Price has contributed greatly to malacology.

Priceconcha tuvuthaensis Solem, spec. nov.

(Figures *2* to *9* and Figures 16, 17a, 19, and 20)

Diagnosis: Shell larger than average, diameter 4.05–4.54 mm (mean 4.29 mm), with $7\frac{1}{8}$+ to $7\frac{5}{8}$ very tightly coiled whorls that increase only slightly in width. Apex and spire strongly elevated, slightly rounded above, body whorl not descending more rapidly, H/D ratio 0.528–0.587 (mean 0.558). Umbilicus broadly "V"-shaped, regularly and evenly decoiling, contained 2.73–3.07 times (mean 2.90) in the diameter, margin strongly rounded at base, sides somewhat flattened internally. Apical whorls and early spire macroscopically and microscopically smooth, with vague radial growth striae visible by fifth whorl, surface on last two whorls with remnants of typical microreticulations (visible at 96X) between stronger radial growth striae. Peripheral keel edge showing crowded remnants of major rib swellings, interstices equal to their width, but swellings too vaguely outlined for counting. Sutures impressed on early spire, becoming progressively shal-

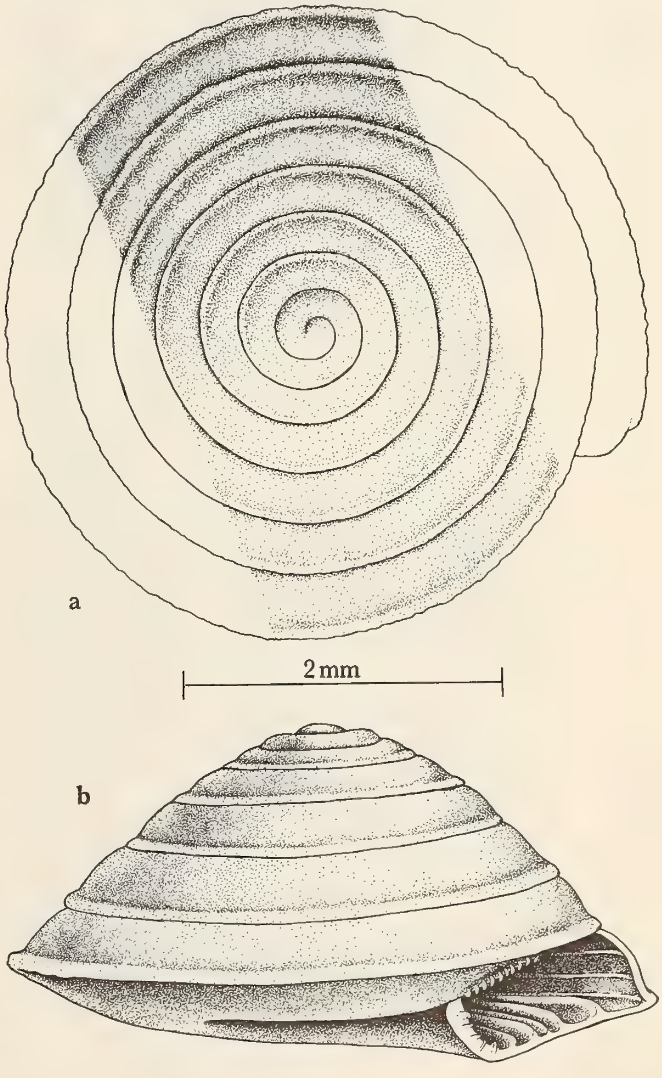


Figure 16

Priceconcha tuvuthaensis Solem, new species.

Holotype. FMNH 168131: *a*, top view of shell; *b*, side view. Scale line equals 2 mm

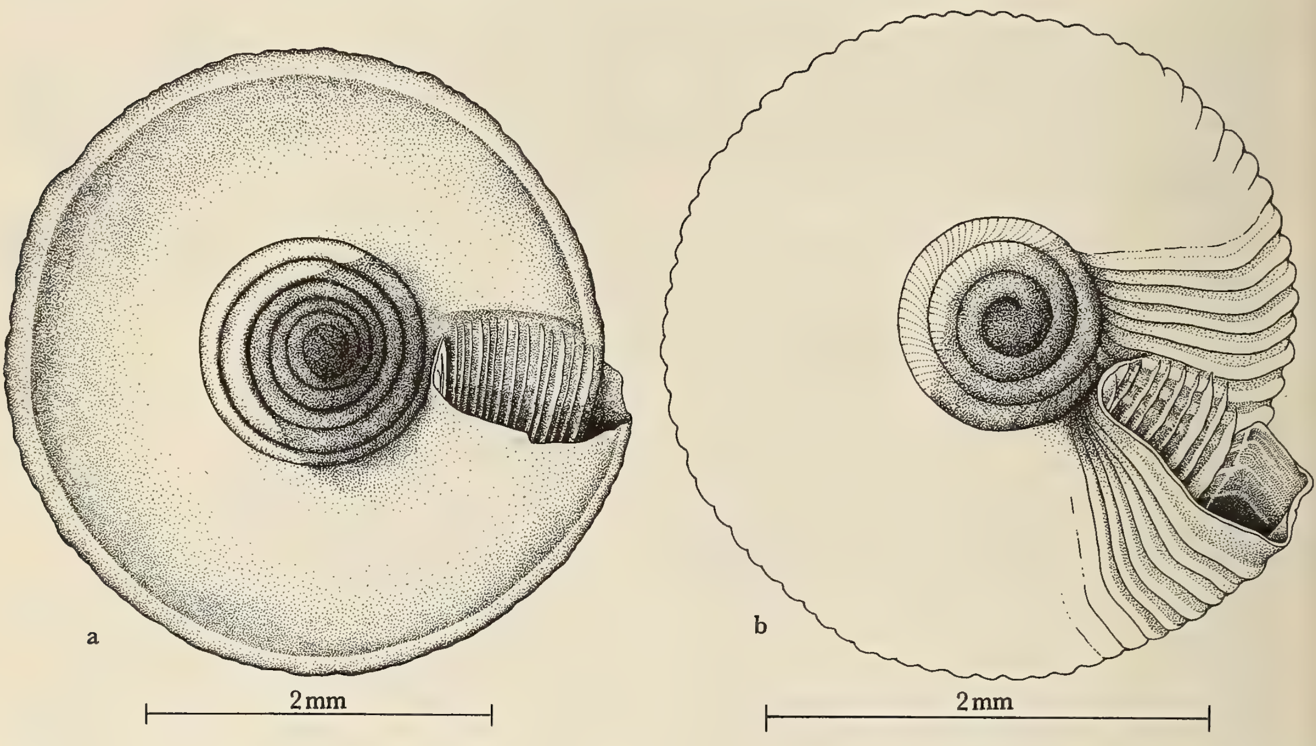


Figure 17

Priceconcha tuvuthaensis Solem, new species.

a. Holotype. FMNH 168131. Bottom view of shell.

Thaumatodon ***spirrhymatum*** Solem, new species

b. Holotype. FMNH 176001. Bottom view.

Explanation of Figures *1* to *4*

Thaumatodon ***spirrhymatum*** Solem, spec. nov.

Figure *1:* Paratype, FMNH 168221. Apical shell sculpture on second whorl showing alternation of major and micro-radials, plus the "squiggly" micro-spirals. X 1 150

Priceconcha tuvuthaensis Solem, gen. nov., spec. nov.

Figures *2–4:* Fragments of dissected paratype, FMNH 168136.
Figure *2:* single bead on palatal barrier viewed from a right, very slightly posterior angle. X 535
Figure *3:* detail of palatal bead surface viewed from directly above. X 2 100
Figure *4:* a 45° angled view of individual denticles on another palatal bead. X 5 850

1

2

3

4

lower. Whorls strongly rounded out to supraperipheral sulcus, followed by protruded, narrow, thread-like keel, lower palatal margin almost flat, columellar margin strongly rounded. Aperture ovate, very strongly flattened laterally below periphery, inclined about 35° from shell axis. Parietal lamellae 4, extending posteriorly for more than 1 full whorl, with 10 or 11 accessory traces: all major parietals very low, lamellar blades, with very gradual anterior descension, separable from traces by the presence of low beads (Figure *1*) that are visible ⅜ of a whorl inside aperture; 4th parietal without beads and recognizable only by being slightly wider than adjacent traces. Accessory traces as long as major lamellae, 1 to 3 between each pair, variable in exact position, with or without a superior lamellar trace, two usually below 4th parietal. Columellar lamellae 2, lying parallel to the plane of coiling, extending posteriorly a full whorl, with gradual anterior descension across callus almost to lip edge. Accessory traces between 1st and 2nd and then below 2nd columellar, traces less than half height of major lamellae, terminating distinctly posterior of major lamellar ending. Palatal lamellae 5, extending posteriorly more than one whorl, with 3 or 4 accessory traces; first 4 palatals subperipheral, progressively increasing in height, with gradual anterior descension, beading deeply recessed and inconspicuous, widely spaced; 5th palatal supraperipheral, located just above keel, a low lamellar ridge without beading on visible portion. Accessory traces located below 1st palatal, between 2nd and 3rd, and one or two located above 5th palatal.

The relatively large size, increased whorl count, very long and numerous apertural barriers, widely open umbilicus, reduced sculpture, and prominent keel easily separate ***Priceconcha tuvuthaensis*** from any species of *Thaumatodon* or the other genera sharing its anatomical peculiarities. Of the generalized endodontid genera, only the larger species of *Nesodiscus* are similar in shape and sculpture reduction. They differ immediately in anatomical features, their very much larger size, and gross reduction in number and prominence of apertural barriers.

Description: Shell larger than average, with slightly more than 7½ tightly coiled whorls. Apex and spire strongly elevated, slightly rounded above, H/D ratio 0.528. Sculpture as in diagnosis. Umbilicus broadly "V"-shaped, regularly decoiling, contained 2.73 times in the diameter. Whorl contour and apertural contours as in diagnosis, except for presence of eleven parietal traces and four palatal traces. Color reddish-yellow horn, without traces of flammulations. Height of holotype 2.14 mm, diameter 4.05 mm.

Holotype: Fiji: Lau Archipelago, Tuvutha Island, west coast in heavy forest on limestone at 100 feet elevation. Collected on trunks of trees during wet spell by Laurie Price on October 2, 1970. Field Museum of Natural History number 168131.

Paratypes: FMNH 168136, 2 specimens.

Description of soft parts: Foot and tail retracted in all examples, so length not measured. Body color yellow-white, no darker markings.

Posterior portion of pallial roof (Figure 19 *b*) with very narrow 2.4 mm long kidney (K), rectal arm reduced in prominence. Heart (H) elongated and very slender, paralleling hindgut. Pulmonary vein (HV) simple and unbranched. Ureter (KD) reflexion partly above fold in kidney, extending to ureteric pore (KX) just anterior of rectal kidney margin and next to hindgut (HG). Posterior margin of kidney deeply indented by intestinal loop (I). Total length of pallial cavity about three-quarters of a whorl. Surface of anterior pallial roof heavily infested with encysted parasites, probably a nematode, as shown in Figure 19 *a*.

Ovotestis (Figure 19 *a*, G) situated well above stomach (IZ) apex, consisting of tightly clustered, palmately clavate alveoli opening into a single collecting tubule which continues on columellar side of intestine (I) as hermaphroditic duct (GD). Latter without kinking (Figure 20 *a*), entering laterally near base of very elongated carrefour (X). Talon (GT) very long and tapering, entering head of carrefour, both partly buried in albumen gland (GG), which, together with the head of the spermatheca (S), lies just apicad of pallial cavity apex. Prostate (DG) and uterus (UT) proportionately short, completely separate tubes only lightly bound together by connective tissue. Free oviduct (UV) section of female tract more expanded than uterine, but state of preservation and heavy parasitization prevented any detailed examination of structural differences. Atrium (Y) short, slightly wider in diameter than free oviduct.

Vas deferens (VD) very long, highly convoluted in part (possibly an artifact of contraction), entering epiphallus (E) through a valve. Epiphallus about two-thirds length of penis, quite thick, internally (Figure 20, *b*) with two high, rather complex pilasters (PP) that continue through penis to atrium, but decrease rapidly in height. Penis (P) about 1.5 mm long, with spermathecal shaft (S) inserting near base. Penial retractor muscle (PR) arising on diaphragm, inserting on junction of epiphallic and penial portion of the terminal duct. Head of spermatheca very slender and elongated.

Radular teeth typical Endodontidae. Central (Figure *5*) tricuspid, slightly larger than 1st laterals. Early laterals (Figure *6*) bicuspid, simple, ectocone more than half

length of mesocone. Upper anterior margin of early laterals with prominent knob behind mesocone. Anterior tooth margin sloping backwards and downwards at about 45° angle to basal plate attachment on radular membrane, slope length about half total tooth length. Posterior basal plate margin with prominent bump in front of ectocone (Figure *6*, upper left) and mesoconal area to receive anterior upper margin of next tooth under stress conditions. Mesoconal supporting ridge large, evenly curved from cusp tip to mid point of tooth height, then curving backwards to join basal plate. Subsequent lateral teeth (Figure 7) developing fine denticulations on the outside edge of the ectocone. During lateromarginal transition (Figure *8*) these denticulations appear also on the outside edge of mesocone. Transition to marginal teeth also marked by distinct development of a narrow, sharp endocone (Figures *8, 9*), frequently with considerable ectoconal splitting. Transition between laterals and marginals occurring over a 3 to 5 tooth area.

Digestive and free muscle systems without unusual features. Entire body heavily invaded by encysted parasites, which are ovate in shape, averaging about 0.2 mm in maximum length. Based on dissection of an adult specimen 4.54 mm in diameter, from FMNH 168136.

Remarks: Two living specimens, an adult and a juvenile, were collected on tree trunks in very damp forest up to 10 feet above ground level. Ascension of a tree trunk is not unprecedented in the family, although highly unusual. A few Hawaiian endodontids and one species of *Libera* from a very wet area on Tahiti have been taken in such arboreal situations, but most of the 180 species level taxa are strictly terrestrial. Quite possibly the remarkable degree of shell sculpture reduction in ***Priceconcha*** correlates with this habitat. Virtually no endodontids as small as ***Priceconcha*** show any significant degree of sculpture reduction (Solem, in press). Elsewhere (Solem, in press) I hypothesize concerning the significance of shell sculpture to a litter dwelling snail. If ***Priceconcha*** has indeed become an essentially arboreal or semiarboreal species, then the virtual loss of the sculpture in a moss habitat becomes less surprising.

The beading on the apertural barriers (Figures *2–4*) is typical in character, although narrower than in most *Thaumatodon* (see Solem, 1973, Figures *11–13*). Elevated denticles on the beads (Figure *2*) are restricted to the posterior raised portion of each bead and are absent from the rest of the barrier edge. Viewed at higher magnifications (Figures *3, 4*), the individual denticles are seen as additive elements to the surface. In all cases the points of the denticles are directed towards the outside of the aperture. In the group of genera including *Thaumatodon,* ***Priceconcha,*** the Palau genus and other new Lau Archipelago genus, such denticles are restricted to the bead surfaces, whereas in other Endodontidae they are found along the upper edge of the major barriers on at least the posterior third to half.

Features of the pallial region and genitalia that differ obviously from those of *Thaumatodon spirrhymatum* should not be assigned major phyletic significance. Essentially all of them are correlatives of the change in whorl width, coiling pattern and thus visceral elongation resulting from the increased whorl count of ***Priceconcha.*** Narrowing of the kidney and reduced rectal kidney arm prominence (compare Figures 19 *b* and 21 *c*), plus the much more tightly coiled intestinal loop relate to the narrow cross-sectional area of the whorl. The longer talon and carrefour in ***Priceconcha*** (Figure 20 *a*) compared with *Thaumatodon* (Figure 19 *b*), and the very striking difference in relative "free oviduct-uterus" length shown in the same figures are other demonstrations of this change. Elongation of the genitalia in ***Priceconcha*** was not uniform, but took place primarily in the region between the end of the prostate and the atrium.

Such patterns of "zonal shifts" are characteristically found in snails with increased whorl counts. They also occur as compacted zones on slugs or semi-slugs, where the visceral hump has been shortened in the course of slug evolution. In neither situation is there any pattern as to which zone of the pallial and terminal genitalia is involved

Explanation of Figures *5* to *9*

Priceconcha tuvuthaensis Solem, gen. nov., spec. nov.

Figures *5–9:* Radular elements from dissected paratype, FMNH 168136.

Figure *5:* central tooth seen from a low posterior angle. X 9 500

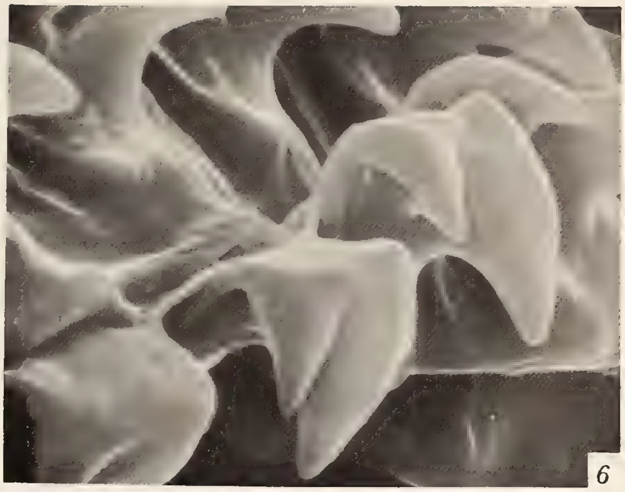
Figure *6:* early lateral teeth on a fold in the radular membrane showing the point of attachment and anterior part of the tooth that is free from the basal membrane. X 5 425

Figure *7:* late lateral teeth viewed from a low, outside angle showing serrations on ectoconal and mesoconal cusp edges. X 9 800

Figure *8:* lateromarginal transition area on left side of radula viewed from a low outside angle. X 4 775

Figure *9:* marginal teeth from right side of radula seen from almost directly above, showing variations in ectoconal splitting. X 8 700

5



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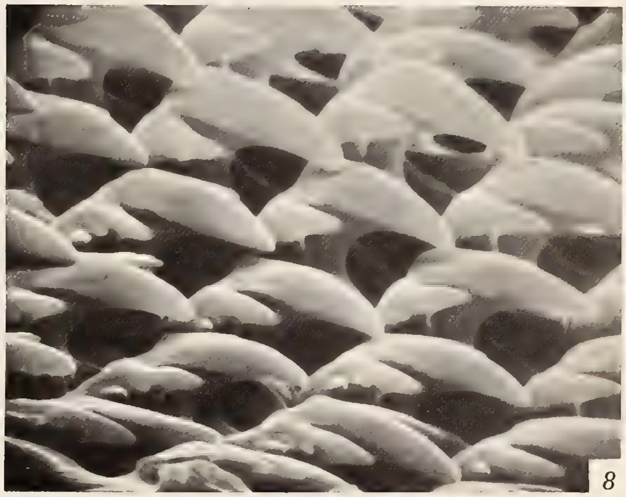
7



8

9

in the zonal shift. It can be any part. Since no *Thaumatodon* are known to occur on Tuvutha, the lack of alterations in penial structure from the basic *Thaumatodon* pattern has no significance.

In summary, ***Priceconcha tuvuthaensis*** is a genus and species characterized by major conchological changes, but only comparatively minor anatomical changes. It also seems to differ in habitat from the vast majority of endodontids.

Thaumatodon Pilsbry, 1893

Manual of Conchology, 2nd series, 9:26

Endodontidae with typical apical and microsculpture, major sculpture enlarged in many species, frequently greatly reduced on body whorl. Apertural barriers with small serrated beads on upper margin, usually several accessory lamellar traces developed. Anatomically characterized primarily by differentiation of an epiphallic zone in the penis and spermatheca inserting on penial side of the peni-oviducal angle.

Type Species: *Pitys multilamellata* Garrett, 1872 by OD.

Including the new species described below, there are nine species that belong to *Thaumatodon* as restricted by Solem (in press). *Thaumatodon multilamellata* (Garrett, 1872) from the Cook Islands, *T. hystricelloides* (Mousson, 1865) from Samoa, *T. decemplicata* (Mousson, 1873) from the Ellice Islands, two undescribed species from Tonga, and four species from the Lau Archipelago of Fiji—*T. subdaedalea* (Mousson, 1870), undescribed species from Wangava and Mango, and the species from Thithia described below as ***Thaumatodon spirrhymatum.*** In addition, the new genus *Priceconcha* and a second undescribed genus from the Lau Archipelago are derivatives of *Thaumatodon*, making this area a major center of diversity. It is highly probable that additional undescribed species exist in Lau. The only other closely related genus is an undescribed taxon from the Palau Islands, which, together with *Thaumatodon, Priceconcha* and the other new genus from Lau, form an anatomically well differentiated, monophyletic section of the family.

Thaumatodon ***spirrhymatum*** Solem, spec. nov.

(Figures *1, 10* to *15* and Figures 17b, 18, and 21)

Diagnosis: Shell large for genus, diameter 2.96 mm–3.45 mm (mean 3.23 mm), with $4\frac{1}{2}$ to $5\frac{3}{8}$ normally coiled whorls. Apex and early spire flat or barely protruding, whorls of lower spire descending much more abruptly, attachment of upper palatal edge along lower margin of peripheral keel after development of latter, H/D ratio 0.441–0.564 (mean 0.494). Umbilicus broadly "V"-shaped, regularly decoiling, contained 3.17–3.92 times (mean 3.53) in the diameter, margin of last whorl very sharply rounded, but not keeled. Apical whorls not differentiated in form or sculpture from postnuclear whorls, sculpture

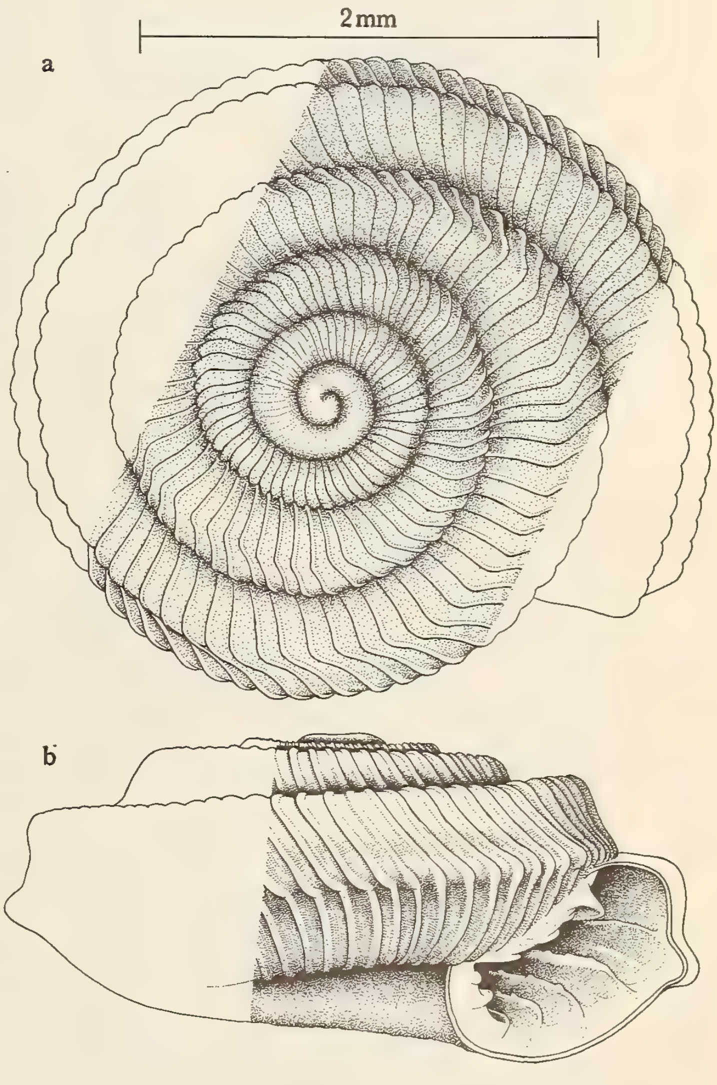


Figure 18

Thaumatodon ***spirrhymatum*** Solem, new species.

Holotype. FMNH 176001: *a*, top view of shell; *b*, side view of shell with parietal lamellar traces omitted. Scale line equals 2 mm

(Figure *1*) consisting of alternating major ribs and microradial ribs, crossed by a microspiral sculpture of typically "squiggly" spiral riblets. On postnuclear whorls, sculpture of high, broad, rounded, slightly protractively sinuated, normally crowded radial ribs, 66–120 (mean 81.3) on the body whorl, whose interstices are one to three times their width. Major ribs become slightly nodose on crossing keels, ribbing often greatly reduced on last eighth to quarter of body whorl. Microsculpture very fine, often eroded from major rib surfaces, a combination of three to eight radial riblets crossed by slightly finer and more crowded spiral riblets. No secondary spiral sculpture. Sutures on early spire deep, on lower spire and body whorl flatly rounded out to a slightly protruding and strongly rounded supraperipheral keel, then concavely rounded to thread-like and strongly protruded peripheral keel, lower palatal wall rather flatly rounded down to sharply rounded columellar margin. Aperture basically ovate, distorted in outline by keels, inclined about 15° from shell axis. Parietal lamellae 4, extending posteriorly beyond line of vision, with four or five accessory traces: upper a very high, thin blade, with four low, narrow beads at widely spaced intervals on posteriorly visible two-thirds of lamella and sharp anterior descension; 2^nd^ much lower, with very gradual descension over anterior third, posterior beading more prominent, spaced at same intervals; 3^rd^ lower than 2^nd^, only three posterior beads visible, very gradual anterior descension; 4^th^ greatly reduced in height, only remnants of beading visible, actually lower than largest trace. Accessory traces between 1^st^ and 2^nd^, 2^nd^ and 3^rd^, 3^rd^ and 4^th^, and below 4^th^ parietal, progressively decreasing in size from top to bottom, with upper trace higher than 4^th^ parietal. A 5^th^ very low and thread-like trace may be located above the upper parietal. Anterior margins of all major lamellae and lamellar traces nearly even. Columellar lamellae 2, lying parallel to plane of coiling, both raised lamellar ridges, upper slightly lower, both crossing peak of columellar callus, but degree of relative anterior extension variable. Palatal lamellae 4, extending posteriorly three-sixteenths of a whorl, with 3 or 4 accessory traces: lower 3 palatals subperipheral, with three moderately prominent beads above on each (Figures *10–12*), lamellae becoming progressively higher with more gradual and longer anterior descension, extending almost to lip edge; 4^th^ palatal just above peripheral keel, a lamellar ridge slightly lower than 3^rd^ palatal, weakly beaded above, with sharp anterior descension. Traces located at columellar-palatal margin, usually a very weak trace between 1^st^ and 2^nd^, more prominent traces between 2^nd^ and 3^rd^, 3^rd^ and 4^th^ palatals.

Thaumatodon ***spirrhymatum*** is immediately recognizable by its bi-keeled body whorl, relatively flat spire and characteristic sculpture. Other Lau Archipelago species such as *T. subdaedalea* (Mousson, 1870), are similar in shape, umbilical width and general appearance, but have rounded body whorls and much different sculpture. Tongan species and the Samoan *T. hystricelloides* (Mousson, 1865) have far narrower umbilici, a much more elevated spire, rounded whorls, wider sculpture that is far more reduced on the body whorl, and much more massive apertural denticles. The Ellice Island *T. decemplicata* (Mousson, 1873) is much smaller in size, has only one columellar tooth, and a rounded periphery.

Description: Shell large, with 4⅝ normally coiled whorls. Apex and early spire slightly protruding, lower whorls descending more rapidly, H/D ratio 0.484. Apical whorls with sculpture partly eroded, sculpture on lower whorls as in diagnosis, body whorl with about 73 rather widely spaced major radial ribs becoming very reduced on last eighth whorl of gerontic growth. Umbilicus broadly "V"-shaped, regularly decoiling, contained 3.17 times in the diameter. Sutures deep on early whorls, shallow when whorl attachment reaches keel base. Supraperipheral keel slightly protruding, rounded, peripheral keel strongly protruding, thread-like. Color yellow-white, with regularly spaced reddish flammulations. Aperture and lamellae as in diagnosis, with trace between 1^st^ and 2^nd^ palatals barely visible. Height of holotype 1.51 mm, diameter 3.13 mm.

Explanation of Figures *10* to *15*

Thaumatodon ***spirrhymatum*** Solem, spec. nov.

Figures *10–15:* Shell fragments and radula from a dissected paratype, FMNH 168221.

Figure *10:* anterior portion of lower palatal lamellar barrier (with nodose beads above) and accessory lamellar traces (no beads above) X 92

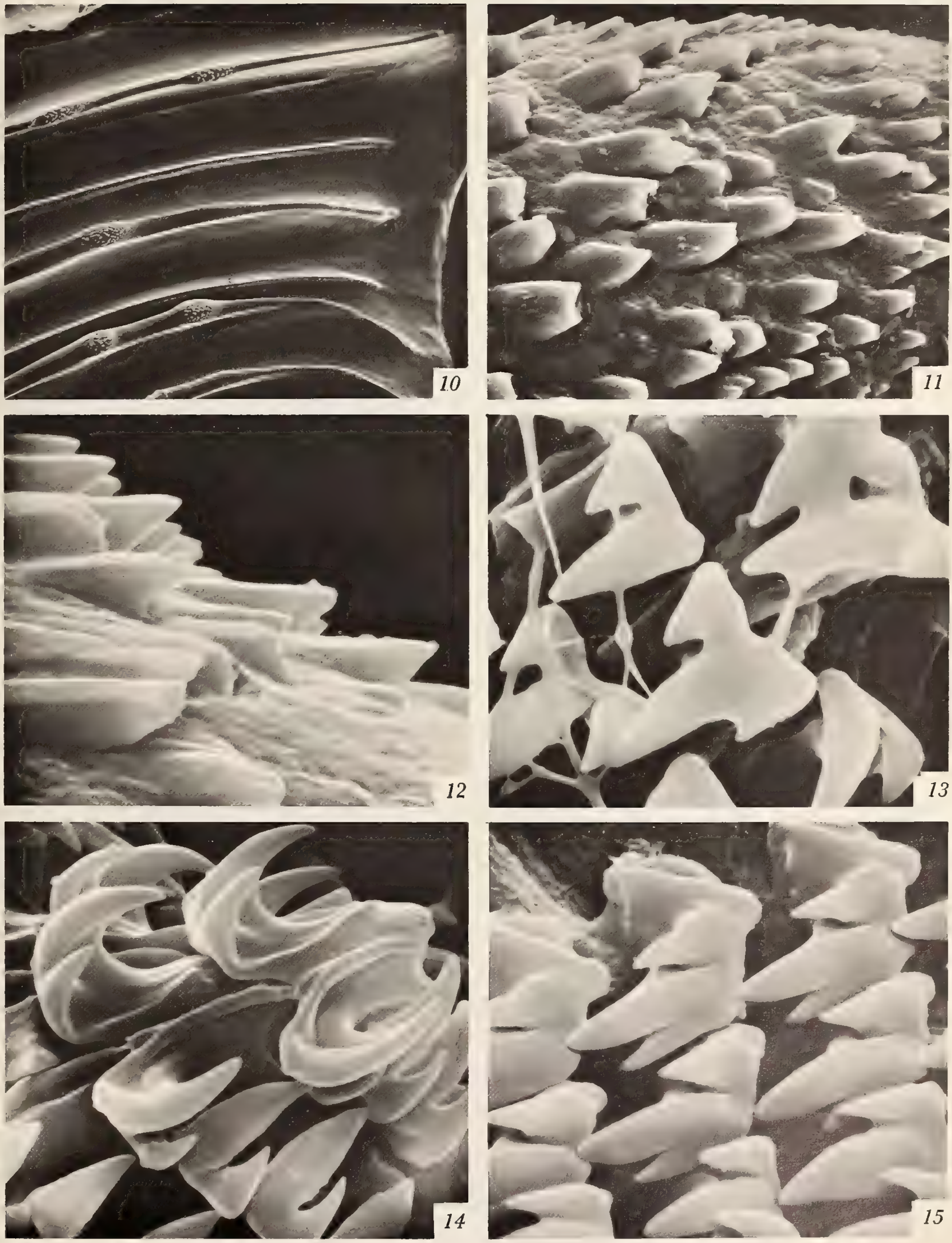
Figure *11:* lateral view of a single lamellar bead on a palatal lamellar barrier. X 1 850

Figure *12:* details of denticles on a bead. X 9 425

Figure *13:* central (tricuspid) and first lateral radular teeth, strands are partly macerated muscle tissue that did not come loose in the sonic cleaner. X 4 750

Figure *14:* lateral teeth from left side of radula near posterior end. X 4 825

Figure *15:* marginal teeth from right side of radula near posterior end. X 5 425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Holotype: Fiji: Lau Archipelago, Thithia Island, Sta. F-9, under rotting wood in deep forest on limestone blocks, near Taruka Village on northwest part of island at 10–100 feet elevation. Field Museum of Natural History number 176001.

Paratypes: FMNH 168221, 36 specimens.

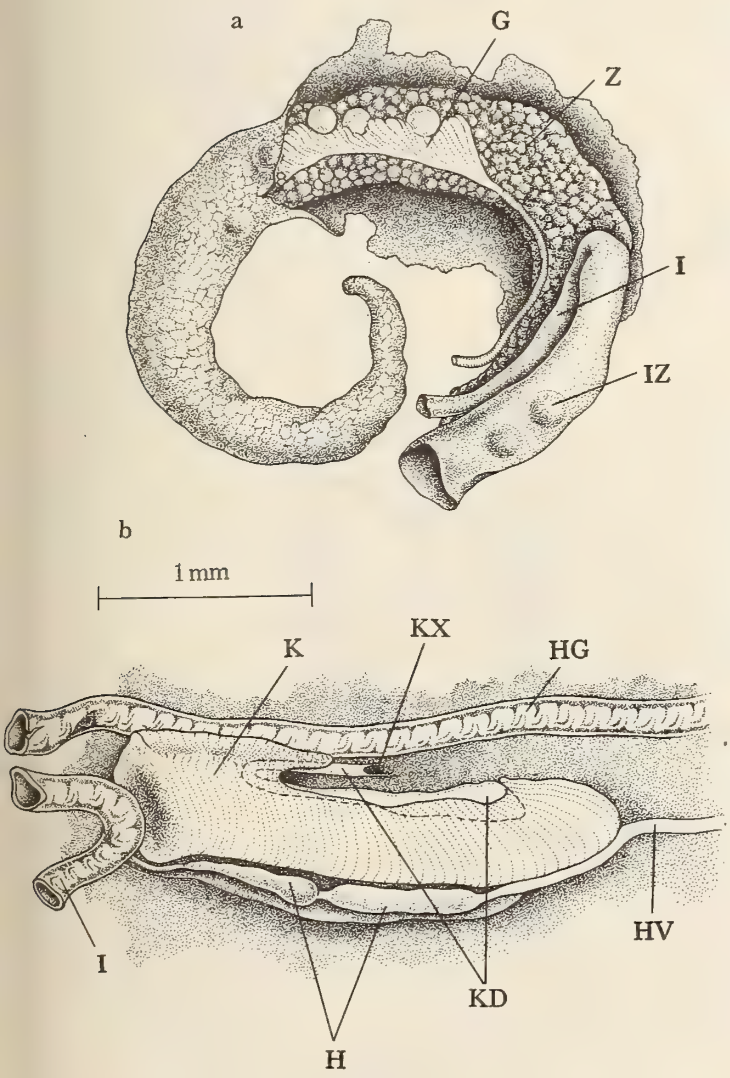

Figure 19

Priceconcha tuvuthaensis Solem, new species.

Paratype. FMNH 168136: *a*, apical genitalia, greatly enlarged; *b*, apex of pallial cavity. Scale line equals 1 mm

Description of soft parts: Foot and tail less than $\frac{2}{3}$ shell diameter in length, truncated anteriorly, bluntly rounded at posterior. Body color yellow-white, no darker markings, eyespots black and prominent. Mantle collar without lobes, no glandular extension onto pallial roof. Position of anus and pneumostome typical.

Pallial roof posterior (Figure 21, c) with rectal arm of kidney (K) slightly more strongly developed than in other dissected *Thaumatodon* and heart (H) more nearly paralleling hindgut (HG). Pericardial arm of kidney about 0.9 mm long, posterior margin deeply indented by and overriding intestinal loop (I). Ureter (KD) reflexed, with ureteric pore (KX) opening slightly anterior to end of rectal kidney lobe. Principal pulmonary vein (HV) simple and unbranched.

Ovotestis (Figure 21, a, G) imbedded in digestive gland above stomach (IZ) apex, composed of more than seven clumps of palmately clavate alveoli that lie at a distinct angle to plane of coiling. They enter a single collecting tubule that continues forward on the columellar side of the reflexed intestine (I) as the hermaphroditic duct (GD). Latter not conspicuously kinked and relatively thin throughout length, entering carrefour (Figure 21, b, X) laterally, with slightly tapered talon (GT) entering carrefour apically. Albumen gland (GG) and head of spermatheca (S) lying above pallial cavity apex, surface of former indented by intestinal loops. Prostate (DG) and uterus (UT) separate tubes for entire length, only lightly held together by connective tissues. Below end of prostatic follicles, uterus expanded into a thicker walled area corresponding to a free oviduct (UV) which continues as a thick-walled, rather muscular tube to the atrium (Y).

Vas deferens (VD) typical, reflexed up peni-oviducal angle, entering head of epiphallus (E) through a valve, distinctly narrower than epiphallus, which is a little more than one-third the length of the 0.52 mm long penis (P). Interior of penis with two longitudinal pilasters extending from epiphallus, one higher than the other. Penial retractor (PR) arising from diaphragm, inserting directly onto head of penis at point where epiphallus curves into penial zone. Spermatheca (S) with elongate, sac-like head next to albumen gland, shaft inserting into base of penis near peni-oviducal angle.

Radula (Figures *13–15*) typically endodontid. Central tooth (Figure *13*) tricuspid, noticeably larger than 1st laterals, anteriorly with sinuated margin. Early lateral teeth (Figure *14*) bicuspid, some indications of weak serrations on outer side of mesoconal cusp. Marginals (Figure *15*) tricuspid, ectocone sometimes with an accessory cusp. Basal plate structure and support system between tooth rows without unusual features.

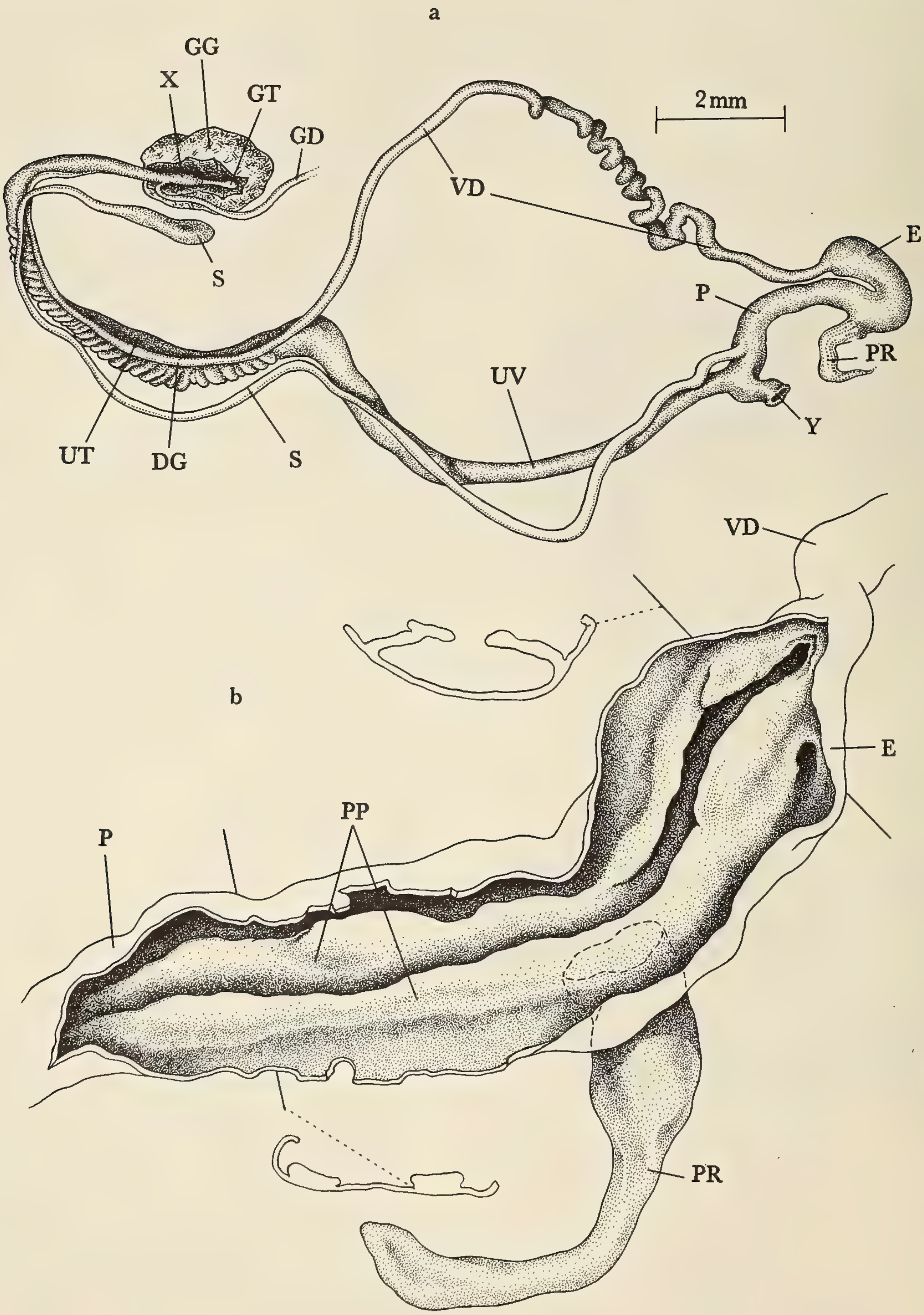

Figure 20

Priceconcha tuvuthaensis Solem, new species.

Paratype. FMNH 168136: *a,* post-apical genitalia with most of hermaphroditic duct omitted; *b,* interior of penial complex showing changing height of pilasters in cross-sectional diagrams. Scale line equals 2 mm

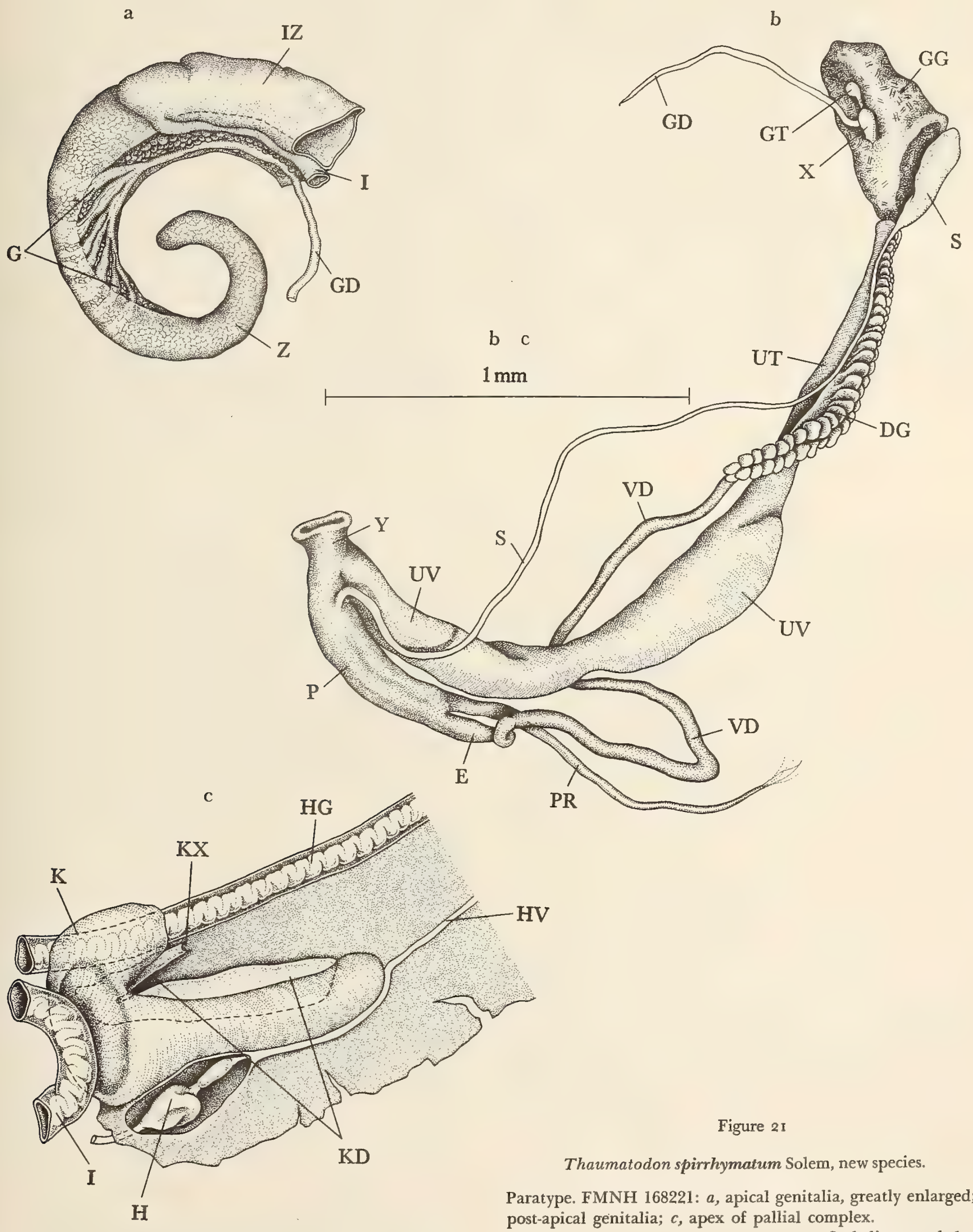

Figure 21

Thaumatodon spirrhymatum Solem, new species.

Paratype. FMNH 168221: *a,* apical genitalia, greatly enlarged; *b,* post-apical genitalia; *c,* apex of pallial complex.

Scale line equals 1 mm

Digestive and free muscle system without unusual features, right ommatophoral retractor passing through peni-oviducal angle. Based on dissection of two adult, fully extended paratypes.

Remarks: Only sixteen out of forty individuals were adult. Variation in the fourteen measured adults is summarized inTable 1.

While details of shell sculpture, size and apertural dentition separate *Thaumatodon* ***spirrhymatum*** from others in its genus, the most dramatic and obvious difference lies in the development of peripheral and supraperipheral keels. This is a relatively common occurrence in the Endodontidae, with species of *Libera* from the Cook and Society Islands, a few *Endodonta* from Hawaii, and scattered undescribed taxa showing an equivalent change. No other *Thaumatodon* shows an indication of keel development and *T.* ***spirrhymatum*** cannot be confused with other members of the genus.

The details of beading on the palatal lamellae are shown on Figures *10–12*. While the beads are at first wider and more prominent (lower part of fig. *10)* than in *Priceconcha,* the denticle structure at equivalent magnification is identical (compare Figure *3* and Figure *11*). In extreme lateral view, the additive nature of the denticles to the barrier surface is clear (Figure *12*).

Radular comparisons show that the marginals in *Priceconcha* (Figure *9*) have far more prominent ectoconal splitting than do those of *Thaumatodon* ***spirrhymatum*** (Figure *15*). Patterns of basal plate structure and interrow support mechanisms are without significant differences. Since the teeth in the two genera were photographed at different angles, they appear somewhat dissimilar, but in actuality are virtually identical.

Table 1

Variation in Shell Size and Shape

Character	Species			
	Thaumatodon ***spirrhymatum*** (14 specimens)		***Priceconcha tuvuthaensis*** (2 specimens)	
	$\bar{X}$ & S.E.M.	Range	$\bar{X}$ & S.E.M.	Range
Shell height in mm	1.59 ± 0.03	1.35 –1.78	2.40 ± 0.26	2.14 –2.66
Shell diameter in mm	3.23 ± 0.04	2.96 –3.45	4.29 ± 0.25	4.05 –4.54
Height/Diameter ratio	0.494 ± 0.008	0.441–0.564	0.558 ± 0.030	0.528–0.587
Whorl count	5.01 ± 0.06	$4\frac{1}{2}$ to $5\frac{5}{8}$	7.40 ± 0.23	$7\frac{1}{8}$+ to $7\frac{5}{8}$
Diameter/Umbilicus ratio	3.53 ± 0.05	3.17 –3.92	2.90 ± 0.17	2.73 –3.07
Ribs on body whorl	81.3 ± 4.23	66 – 120	NONE	

SUMMARY

A new genus and species, ***Priceconcha tuvuthaensis,*** from Tuvutha Island and a previously undescribed species, *Thaumatodon* ***spirrhymatum*** from Thithia Island, both in the Lau Archipelago of Fiji, are described. Details of anatomical structure and scanning electron microscope photos of shell features and radular teeth are presented. The phyletic position of these taxa within the Family Endodontidae is reviewed.

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In press. Entodontoid land snails from Pacific Islands. Part I. Family Endodontidae. Fieldiana: Zoology.

New Fossil Ashmunellas from New Mexico

(Gastropoda : Pulmonata : Polygyridae)

BY

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(1 Plate; 1 Text figure; 1 Table)

FIVE SPECIES OF fossils of the land snail genus *Ashmunella* (Polygyridae) are described herein from New Mexico. One species is from the Rio Grande Valley of Doña Ana County and the others from the Sacramento Mountains, Lincoln and Otero Counties. All are judged to be of Pleistocene age.

The Sacramento Mountains of south-central New Mexico (see Map) are a block-faulted range, extending 60 miles (97 km) north to south and 45 miles (73 km) east to west. On the western side, fault scarps produce sharp relief of over 5000 feet (1524 m) from the desert floor of the adjacent Tularosa Basin (4000 - 5000 feet – 1219 - 1372 m) to the crest of the range (9100 - 9600 feet – 2774 - 2926 m). From the crest, which is thickly forested, the surface slopes gradually towards the Pecos River Valley to the east. Northward, the range merges topographically with the Sierra Blanca Mountains (see Map), a higher mountain mass of igneous rocks. Bedrock of the Sacramento Mountains is almost entirely of Paleozoic sedimentary rocks, preponderantly of Pennsylvanian or Permian age. Permian limestones are especially widespread with most of the crest and eastern slope being capped by limestone rocks of the San Andres Formation. The highly calcareous soils seem to favor an abundance of land snails.

Several canyons dissect the range. In Pleistocene and Holocene times, there have been episodes of both filling and downcutting along these canyons. Some remnants of canyon fill remain as discontinuous, valley-flanking terraces. Some of the fossil snails described here are from such sediments. Others are from colluvial deposits that formed mainly on slopes of valley walls seemingly during times of increased frost activity, judging by the great quantities of angular bedrock fragments contained in the colluvium (GALLOWAY, 1970). In places, colluvial and alluvial deposits seem to interdigitate, suggesting a common causative mechanism.

Localities are listed at the end of each description and identified by a number, in sequence. Numbers of types and paratypes follow locality descriptions. (ANSP = Academy of Natural Sciences of Philadelphia; CAS = California Academy of Sciences).

Ashmunella ruidosana Metcalf, spec. nov.

(Figures *1, 2*)

Description of Holotype: Shell elevated (for genus), rounded peripherally; last whorl descending to aperture; lower lip impinging upon the umbilicus for approximately one half of umbilical width; aperture obliquely semilunar; tridentate; parietal callus relatively thick, bearing a single parietal tooth, which is oblique, straight, evenly rounded on both ends; peristome thick inwardly, bearing teeth in palatal and basal positions; outer tooth long, flat-topped; basal tooth bifid, consisting of two rounded tubercles conjoined medially; tightly whorled embryonic whorl smooth, succeeding $3\frac{1}{2}$ whorls finely and evenly striate, grading to low but progressively larger ribs on last $1\frac{1}{2}$ whorls; finely incised spiral striae transect growth striae on base of shell. Dimensions in Table 1.

Variation: Shells from localities 1 and 3 (see below) are of approximately the same size, averaging, respectively, 13.5 and 13.0 mm in diameter (see Table 1). Specimens from Locality 2, located stratigraphically approximately 40 feet (12.2 m) above locality 3 average larger (14.9 mm diameter for 5 specimens). There is much variability in the basal tooth, which may exhibit (1) two equal-sized tubercles sometimes sufficiently separated to suggest two small, twinned teeth (rare); (2) an outer tubercle slightly larger than the inner (common); (3) the inner tubercle reduced to a sloping callus (frequent) and (4) tubercles so low that a tooth is barely discernible (rare). The palatal tooth is variable in length (Table 1) and in a few specimens appears to comprise 2 or 3 small tubercles similar to those seen in the basal tooth. Width of the umbilicus is variable, depending on the extent to which it is impinged

Table 1

Some measurements and proportions for holotypes (Holo) and paratypes (Para) of five species of fossil *Ashmunella*. For species bearing two parietal teeth, length of only the lower one is shown and in species with two basal teeth, width of only the inner one is given. Means are above, extremes below for the paratypes.

Species (Kind of Type) (Locality Number)			No. of Specimens	Diameter	Height	Parietal Tooth L.	Palatal Tooth L.	Inner Basal Tooth W.	Diameter/ Width of Umbilicus	No. of Whorls
Ashmunella										
ruidosana	(Holo)	(1)	1	14.3	8.8	2.0	2.2	1.7	9.73	6.0
ruidosana	(Para)	(1)	30	13.5	7.9	2.4	2.0	1.5	10.80	5.8
				(12.2 - 14.7)	(6.7 - 9.1)	(1.8 - 3.0)	(1.3 - 2.6)	(1.2 - 1.9)	(7.06 - 14.7)	(5.5 - 6.2)
ruidosana	(Para)	(2)	5	14.9	8.3	2.5	2.6	1.7	7.4	6.2
				(13.7 - 15.5)	(6.8 - 9.4)	(2.3 - 2.7)	(2.2 - 3.0)	(1.5 - 2.1)	(6.5 - 8.6)	(5.8 - 6.4)
ruidosana	(Para)	(3)	10	13.0	7.3	2.2	1.9	1.4	9.7	5.8
				(12.1 - 13.7)	(6.9 - 8.3)	(2.0 - 2.5)	(1.6 - 2.2)	(1.3 - 1.7)	(8.3 - 11.3)	(5.6 - 6.1)
tularosana	(Holo)	(4)	1	14.8	6.6	2.7	2.0	1.4	4.77	5.8
tularosana	(Para)	(4)	25	14.2	6.6	2.5	2.0	1.2	4.95	5.6
				(13.1 - 15.7)	(5.7 - 7.2)	(2.0 - 3.1)	(1.0 - 2.5)	(1.0 - 1.6)	(4.4 - 5.6)	(5.3 - 5.9)
jamesensis	(Holo)	(5)	1	11.9	5.7	2.5	1.7	1.3	7.0	5.5
jamesensis	(Para)	(5)	1	11.7	6.0	2.5	1.1	1.4	7.8	5.5
tegillum	(Holo)	(6)	1	13.2	5.4	2.4	1.5	1.1	5.8	5.6
tegillum	(Para)	(6)	20	12.2	5.3	2.4	1.7	1.1	7.1	5.5
				(11.3 - 13.0)	(4.6 - 6.0)	(1.9 - 3.0)	(1.2 - 1.8)	(0.9 - 1.3)	(5.7 - 9.2)	(5.3 - 5.9)
tegillum	(Para)	(7)	5	11.7	5.0	2.7	1.6	1.1	6.9	5.4
				(11.0 - 12.6)	(4.3 - 5.5)	(2.5 - 2.8)	(1.4 - 1.8)	(1.0 - 1.2)	(6.0 - 7.9)	(5.3 - 5.8)
tegillum	(Para)	(8)	10	10.8	4.8	1.2	1.6	1.0	5.3	5.1
				(10.3 - 11.4)	(4.3 - 5.1)	(0.8 - 1.8)	(1.1 - 1.8)	(0.8 - 1.1)	(4.9 - 6.1)	(4.8 - 5.4)
hawleyi	(Holo)	(9)	1	14.6	7.5			1.5	5.03	5.0

upon by the lip. Its width (taken from point of maximum extension of the lip to opposite umbilical wall) averages 1.37 mm for 10 specimens from Locality 3 and 1.27 mm for 30 specimens from Locality 1. Width of umbilicus in diameter of shell is indicated in Table 1.

Comparisons: Of named, living species of *Ashmunella*, ***A. ruidosana*** seems closest to *A. thomsoniana* (Ancey, 1887) of the southern Sangre de Cristo Mountains, New Mexico ("SCM" in Map), located 155 - 175 miles (250 to 280 km) north of the Ruidoso area. There is a general resemblance in size, shape, sculpture, and in the tridentate condition of the aperture. However, the shell of *A. thomsoniana* is more depressed and the umbilicus wider. The teeth of the outer lip are, as in ***A. ruidosana***, highly variable in size but, on the average, less well developed. A tendency towards further reduction of the denticles seems to be shown by *A. pseudodonta* (Dall, 1897) of the Capitan-Patos-Carrizo Mountains complex ("CM" on the Map), north of the Sierra Blanca Mountains and in ***A. hawleyi***, described below.

Ashmunella ***ruidosana*** and the other species described herein differ from members of the *A. rhyssa* (Dall, 1897) complex, presently widespread in the Sacramento and Sierra Blanca Mountains, in the presence of more and better developed denticles. Shells of a toothless *Ashmunella*, seemingly of the *A. rhyssa* group, occur with ***A. ruidosana***. Therefore, any time in which a common ancestor of the two existed must greatly antedate the age of these deposits.

Etymology: From "ruidoso," Spanish, adjective, "noisy," name applied to the river valley in which the sediments occur, to the nearby Ruidoso River, and to the villages of Ruidoso and Ruidoso Downs. **Type locality** is in Ruidoso Downs.

Localities: (No. 1). **Type Locality**. Lincoln County, NW-$\frac{1}{4}$, SW-$\frac{1}{4}$, NW-$\frac{1}{4}$, Sec. 29, T. 11 S, R. 14 E. 6440 feet (1963 m) elevation. Exposure (in cut) on S side of U. S. Highway 70, opposite "D" in word "Ditch" on Ruidoso Downs 7.5 min. topogr. quadr., 1963, and opposite Ruidoso Downs racetrack. Specimens are abundant in middle part of exposure, *ca.* 20 feet (6 m) above level of highway. Sediments are predominantly light brown (5YR 6/4) silts with scattered angular to sub-rounded gravels. (Rock-colors from Rock-Color Chart of The Geological Society of America).

Holotype: ANSP 325522; **Paratypes:** ANSP 325524; CAS 52677.

(No. 2). This locality is 100 feet (30 m) south of and 30 feet (9 m) higher than Locality 1, located in south wall of a borrow pit (for road fill). The sediments are seemingly conformable with and overlie those mentioned in Locality 1. **Paratypes:** ANSP 325530.

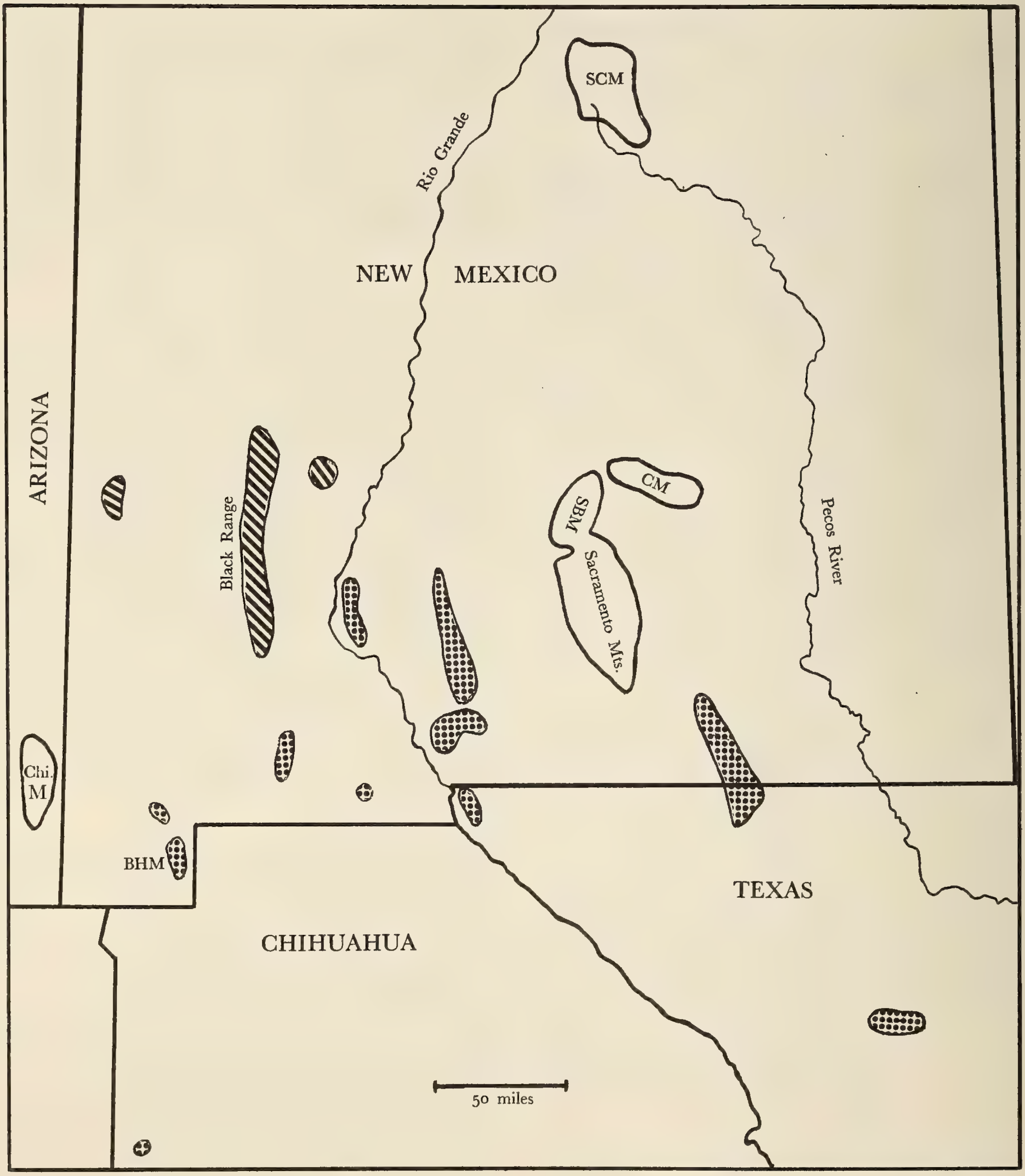
(No. 3). Lincoln County, NE-$\frac{1}{4}$, NE-$\frac{1}{4}$, SE-$\frac{1}{4}$, Sec. 21, T. 11 S, R. 14 E. 6420 feet (1957 m) elevation. This is another cut along U. S. Highway 70, 1.8 miles (2.9 km) NE of Localities 1 and 2. Locality is 0.12 miles (190 m) N of "5" in "6325" benchmark designation on Ruidoso Downs 7.5 min. quadr. Locality is in sediments similar to those at Locality 1. *Ashmunella* ***ruidosana*** occurs sparingly in the lower part of the exposure. **Paratypes:** ANSP 325534.

Ashmunella ***tularosana*** Metcalf, spec. nov.

(Figures *3, 4*)

Description of Holotype: Shell moderately depressed, periphery angular with angle descending on body whorl and becoming obsolete distally; body whorl itself descending only slightly; umbilicus contained 5.8 times in diameter; aperture obliquely oriented, bearing 4 teeth; parietal tooth oblique, long, simple, rising abruptly proximally but descending gradually to a low, slightly sinuous "tail" distally; palatal tooth long, low, flat-topped; basal lip with 2 teeth, laterally compressed, the outer one slightly larger, the two connected by a low callus; distance between two basal teeth equivalent to one-half distance between outer basal tooth and palatal tooth; lip thick, expanded, grooved behind and slightly recurved; parietal callus thin; first $1\frac{1}{2}$ whorls minutely wrinkle-pustulose, succeeding whorls finely striate with a few low ribs immediately behind lip; well-impressed, fine spiral striae on base of shell and on upper surface of last two whorls. Dimensions in Table 1.

Comparisons and Variations: *Ashmunella* ***tularosana*** seems to bear little resemblance to any known species, living or fossil, from the region east of the Rio Grande Valley. Its shell morphology seems close, however, to quadridentate races of the *A. tetrodon* Pilsbry & Ferriss, 1915 complex from the Mogollon, Black, and San Mateo Mountains west of the Rio Grande in New Mexico (see Map). Shells of ***A. tularosana*** seem to occupy a position intermediate in morphology between those of *A. tetrodon tetrodon* and *A. t. animorum* Pilsbry & Ferriss, 1917. It resembles the former more in size of the basal teeth and the latter in position of the teeth, the two teeth being closer to each other and farther from the tooth of the outer lip in *A. t. animorum* than in *A. t. tetrodon*. However, there is some variation in these characters in *A.* ***tularosana*** among the specimens available, with the inner basal tooth being smaller in some specimens. Spiral striae


SCM
Rio Grande
NEW MEXICO
ARIZONA
Black Range
CM
SBM
Sacramento Mts.
Pecos River
Chi. M
BHM
CHIHUAHUA
TEXAS
50 miles

seem more deeply impressed in *A. **tularosana*** than in *A. tetrodon* subspec.; possibly the process of preservation involving *A. **tularosana*** has emphasized this character.

Etymology: From "Tularosa," Spanish, adjective derived in turn from "Tule," a rush or reed. Probably the reed originally referred to was *Phragmites communis* von Trinius, 1820, which still grows along the Tularosa River in places.

Locality: (No. 4). Otero County, SE-$\frac{1}{4}$, SW-$\frac{1}{4}$, SE-$\frac{1}{4}$, Sec. 19 T. 14 S, R. 13 E. 7440 feet (2268 m) elevation. Exposure in road cut on east side of Tularosa Canyon Road on east side of upper Tularosa River, 0.6 mile (970 m) S of Firman Canyon Road (leading to east) and 1.4 miles (2.26 km) N of road to Mescalero Apache Industrial Park (leading to west). Sediments predominantly of angular, unsorted limestone cobbles. Grayish orange-pink (5YR 7/2) silt, in which *Ashmunella **tularosana*** occurs, fills interstices among the cobbles. Seemingly the species inhabited a talus of angular stones as do many modern members of the genus. Shells were entombed by silts that accumulated in interstices. *Ashmunella **tularosana*** seems to have aggregated in groups (as do modern *Ashmunella* in many instances observed). Seemingly these groups were killed (or died) and were buried *in situ.* Thus, if one specimen is located in place, careful digging usually reveals other shells nearby. The exposure can most readily be located by searching for the associated shells of a carinate *Oreohelix,* which are more numerous and easily located. **Holotype:** ANSP 325529; **Paratypes:** AN SP 325535; CAS 52680.

*Ashmunella **jamesensis*** Metcalf, spec. nov.

(Figures *5, 6*)

Description of Holotype: Shell depressed; periphery angular with angle slightly above center on body whorl; body whorl descending only slightly to aperture; umbilicus narrow, contained 5½ times in shell diameter; aperture subquadrate in shape, obliquely oriented, bearing 5 teeth; thin parietal callus bears 2 parietal teeth, these arising deeply within aperture (so deeply that their area of origin cannot be clearly seen from aperture); lower tooth longer, descending obliquely from point of origin, terminating in a short, low callus oriented towards the columella; upper parietal tooth horizontal (parallel to plane of whorls), highest proximally, tapering to a low ridge distally; 3 teeth in outer lip with interdental intervals and distance from lowest tooth to lower terminus of lip all approximately equal; upper tooth situated deeply within lip, obliquely oriented, flat-topped; lower 2 teeth high, relatively massive, laterally compressed (not joined by intervening callus), middle tooth larger than lower one; lip peristome especially thick, expanded and reflected with a deep groove behind it; embryonic 1½ whorls smooth; succeeding whorls finely striate except for last half of body whorl, which is moderately striate; a few fine spiral striae barely discernible around periphery of body whorl. Dimensions in Table 1.

Variation: Only 3 complete and a few fragmentary specimens were found (all from Locality 5). Teeth show little variation. Spiral striae are better developed on other specimens than on the holotype.

Comparisons: *Ashmunella **jamesensis*** resembles *A. mearnsi* (Dall, 1895) of the Big Hatchet Mountains, southwestern New Mexico. In the group of *A. mearnsi,* Pilsbry (1940: 973 - 979) included several species. A number of additional species, seemingly of this group, have subsequently been described from the mountains of southcentral New Mexico south of the Sacramento Mountains, from Trans-Pecos Texas, and from northwestern Chihuahua, Mexico (see Map). Within this group, *A. mearnsi* and *A. **jamesensis**,* peripheral species geographically, are perhaps primitive in regard to shell morphology.

Locality: (No. 5). Otero County, NE-$\frac{1}{4}$, NW-$\frac{1}{4}$, NW-$\frac{1}{4}$, Sec. 21, T. 16 S, R. 14 E. 6920 feet (2109 m) elevation. Walls of a large borrow pit immediately north of U. S. Highway 82, *ca.* 3 miles (4.8 km) W of Mayhill, 0.7 mile (1.13 km) W of James Canyon Campground, and opposite New Mexico State Highway Department facilities. Borrow pit is extensive, covering approximately 1 acre (approximately 4046 m^2); it is presently inoperative but was formerly utilized to obtain road fill for U. S. Highway 82. Cuts in the quarry reach 60 feet (18.3 m) in height and *Ashmunella jamesensis* occurs approximately halfway between top and bottom in the eastern, more gently sloping part of the quarry. Sediments are predominantly light brown (5YR 5/6) silts with several lenses

(← on facing page)

Map (southwestern United States and adjacent Mexico) indicating geographic features mentioned in the text. Dotted pattern indicates mountains known to be inhabited by members of the *Ashmunella mearnsi* (Dall, 1895) group. Obliquely striped pattern indicates mountains inhabited by the *Ashmunella tetrodon* Pilsbry & Ferriss, 1915, group. BHM = Big Hatchet Mountains; CM = Capitan Mountains; Chi M = Chiricahua Mountains; SBM = Sierra Blanca Mountains; SCM = southern Sangre de Cristo Mountains.

of highly cemented angular to subrounded conglomeratic gravels. Fossils of a large *Oreohelix* abound; *A. jamesensis* is extremely rare. **Holotype:** ANSP 325531; **Paratypes:** ANSP 325526; CAS 52676.

Ashmunella ***tegillum*** Metcalf, spec. nov.

(Figures *7, 8*)

Description of Holotype: Shell compressed, strongly keeled peripherally, keel approximately midway of height of shell, body whorl not descending; umbilicus deep, narrow, contained 5.6 times in shell diameter; aperture oblique, distal and dorsal margins straight, ventrolateral margin broadly rounded; parietal callus thick, continuous with lip peristome, slightly raised and shelflike along outer (distal) margin, bearing 2 teeth that arise proximally on exposed part of callus (that is, not deep-set), teeth not connected; lower parietal tooth obliquely oriented, slightly sinuous, surface roughened in places; upper parietal tooth a low ridge, horizontally oriented, *ca.* $\frac{3}{4}$ as long as lower tooth and much lower, slightly higher proximally, tapering distally and merging with parietal callus; lip peristome thick, expanded, greatly reflected at an angle of *ca.* 30°; deep narrow groove between reflected peristome and body whorl, peristome bearing 3 teeth; upper lip tooth obliquely oriented, arising from inner part of peristome, rectangular with flat top; middle tooth laterally compressed, closer to upper than to lower tooth; lower tooth less compressed, more tubercular, approximately equidistant from middle tooth and from lower terminus of lip; embryonic $1\frac{1}{2}$ whorls with exceedingly fine striae, next whorl with minute, reticular wrinkles (possibly having borne hairs or scales in life), remaining whorls with growth striae becoming progressively coarser distally and riblike on last part of body whorl; entire lower surface of shell with sinuous ribs, these becoming coarser distally; sparse spiral striae impressed on lower surface of shell and dorsal surface of body whorl and around keel; distinctive raised carina rises along inner side of suture on third whorl, continuing on to become peripheral keel; carina and keel scalloped on inner side because of overlapping festoons of shell increment.

Variation: Among specimens from Localities **6** and **7**, there is relatively little variability and that mainly in the degree of sculpturing (striate to ribbed) and in tooth shape. The lower parietal tooth varies from markedly sinuous to almost straight. The upper parietal tooth, although present in all specimens, shows various degrees of development. In one specimen the lower lip tooth is bifid. Since it seems likely that the two basal teeth originally arose from such a bifid single basal tooth (as in *Ashmunella ruidosana,* described above), it is of interest that this tendency again appears in shells already possessing 3 teeth in the outer lip.

Specimens from Locality **8** are smaller than those from Localities **6** and **7** (Table 1) and the lip peristome is thinner and teeth are less well developed on the former specimens. The lower parietal tooth is shorter and straighter and an upper parietal tooth was observed in only one of 15 specimens. The lip teeth are relatively smaller and the upper tooth is rounded rather than rectangular as in most specimens from Localities **6** and **7**. Possibly the smaller, weakly denticulate shells from Locality **8** are dwarfed in response to an adversely cold climate to which they were subjected. They occur 1500 - 1600 feet (465 to 490 m) higher than specimens from Localities **6** and **7**. Dwarfing is presently observable in specimens of *Ashmunella rhyssa* living at relatively higher altitudes in the same mountains.

Comparisons and Discussion: The compressed shell with (usually) 2 parietal teeth suggests that this species, like *Ashmunella jamesensis* (above) probably belongs to

Explanation of Figures *1* to *12*

(Dimensions in Table 1; ANSP = Academy of Natural Sciences of Philadelphia)

Figures *1, 2*: Holotype, *Ashmunella* ***ruidosana*** Metcalf, spec. nov., ANSP 325522

Figures *3, 4*: Holotype, *Ashmunella* ***tularosana*** Metcalf, spec. nov., ANSP 325529

Figures *5, 6*: Holotype, *Ashmunella* ***jamesensis*** Metcalf, spec. nov., ANSP 325531

Figures *7, 8*: Holotype, *Ashmunella* ***tegillum*** Metcalf, spec. nov., ANSP 325528

Figures *9, 10*: A specimen of *Ashmunella ferrissi* Pilsbry, 1905, from Arizona, Cochise County, Chiricahua Mountains, Cave Creek Canyon, 0.3 mile (0.49 km) north of its junction with South Cave Creek Canyon

Figure *11*: Paratype, *Ashmunella* ***hawleyi*** Metcalf, spec. nov., ANSP 325526

Figure *12*: Holotype. *Ashmunella* ***hawleyi*** Metcalf, spec. nov. ANSP 325527

Figure *1*

Figure *3*

Figure *5*

Figure *2*

Figure *4*

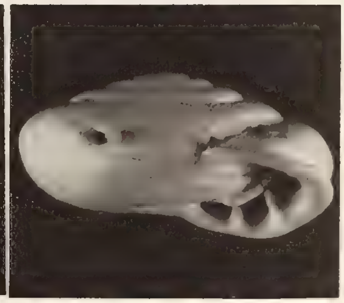


Figure *6*

Figure *7*

Figure *9*

Figure *11*

Figure *8*

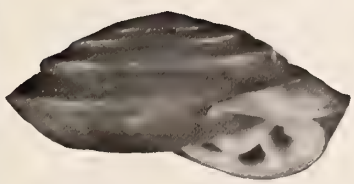


Figure *10*

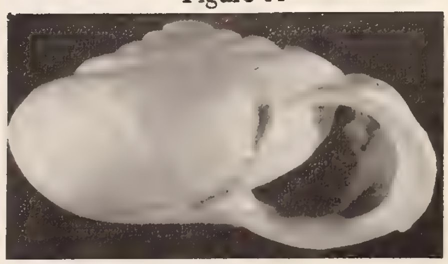


Figure *12*

the *A. mearnsi* group (PILSBRY, 1940: 972). However, among living species, the shell is, surprisingly, in general appearance closest to that of *A. ferrissi* Pilsbry, 1905, of the Chiricahua Mountains, southwestern Arizona (see Map). The strongly carinate, almost turreted shell (Figure *10*) makes these two species perhaps the most distinctive in appearance of known species of *Ashmunella*. However, the species differ in several ways: *A. ferrissi* seems never to possess an upper parietal tooth; *A. ferrissi* is almost smooth below, while *A. **tegillum*** is coarsely sculptured; and *A. ferrissi* possesses a higher spire than does *A. **tegillum*** (Figures *7 - 10*). Also weighing against the possibility of close relationship of the two is the considerable distance of *ca.* 220 miles (355 km) between the Sacramento and Chiricahua Mountains. I deem it likely that the similarities between the two species are, in this case, attributable to parallel evolutionary trends in two different mountain ranges. It seems probable that *A. ferrissi* evolved *in situ* in the Chiricahua Mountains from a less carinate and less turreted ancestor like *A. angulata* Pilsbry, 1905, which occurs nearby.

Etymology: Latin, substantive, diminutive of *tegulum,* a roof. Epithet refers to resemblance of upper part of shell to a small, round thatched roof.

Localities: (No. 6). **Type Locality**. Otero County, NE-¼, SW-¼, SW-¼, Sec. 30, T. 17 S, R. 14 E. 7250 feet (2209 m) elevation. Gravel quarry on N side of Agua Chiquita Canyon Road, 0.65 mile (*ca.* 1 km) E of center of village of Sacramento. Quarry covers *ca.* ½ acre (*ca.* 2023 m^2) and has been cut back into the valley slope to a height of 70 - 80 feet (21 - 24 m) above Agua Chiquita Canyon Road. *Ashmunella **tegillum*** occurs at several levels, but most abundantly in the northwest part (in 1972) of the quarry, 30 feet (9 m) below top of exposed section. Holotype was collected in this area. Sediments are predominantly limestone gravels and cobbles, with interstices filled with grayish orange-pink (5YR 7/2) silt in which *A. **tegillum*** occurs along with *A. rhyssa*. **Holotype:** ANSP 325528; **Paratypes:** ANSP 325533; CAS 52678.

(No. 7). Otero County, SE-¼, SW-¼, SW-¼, Sec. 3, T. 17 S, R. 13 E. 7300 feet (2225 m) elevation. Exposure in road cut on SW side of road from Peñasco to Agua Chiquita Canyons, 0.4 mile (650 m) SW of its junction with Peñasco Canyon Road. Cut is in a high terrace along S wall of Peñasco Canyon, in sediments of heterogeneous nature, seemingly mixed alluvium and colluvium. Strata of unsorted, angular limestone cobbles and gravels are interbedded with massive silts and lenses of subrounded limestone gravels. *Ashmunella **tegillum*** occurs in light brown (5YR 6/4) silts that fill interstices of the angular gravels. **Paratypes:** ANSP 325521.

(No. 8). Otero County, SW-¼, NW-¼, SW-¼, Sec. 35, T. 17 S, R. 11 E. 8850 feet (2697 m) elevation. Exposure in road cut on NE side of Sacramento Canyon Road, 0.5 mile (800 m) SE of its junction with the road from Cloudcroft to Sacramento Peak Observatory. Sediments are hillslope colluvium, predominantly of angular limestone gravels, resting on Permian limestone bedrock, which is exposed in lower part of cut. Gravels are cemented into a conglomerate in lower part. Moderate brown (5YR 4/4) silts fill interstices of the cobbles. *Ashmunella **tegillum*** occurs in these silts along with *A. rhyssa* and *Oreohelix socorroensis socorroensis* Pilsbry, 1905. **Paratypes:** ANSP 325525; CAS 52679.

Specimens of *Ashmunella **tegillum**,* less abundant than at the above localities were also taken at 4 other localities in the southern Sacramento Mountains.

*Ashmunella **hawleyi*** Metcalf, spec. nov.

(Figures *11, 12*)

Ashmunella sp., METCALF, 1967, Sci. Ser., Univ. Texas at El Paso, 1: 49 - 51; figs. 1, 2 (Discussion and figures given, but shell not described)

Description of Holotype: Shell moderately elevated for genus; whorls full and rounded peripherally, last whorl descending to aperture; lower lip flaring slightly out over umbilicus; aperture obliquely semilunar; parietal callus relatively thick, bearing a low, straight obliquely oriented swelling in the position of a parietal tooth, basal tooth low, bifid, consisting of 2 conjoined, tubercular swellings; embryonic whorl smooth, succeeding whorls with fine growth striae and a few coarse striae appearing on last ⅓ of body whorl; obscure fine spiral striae occur on base and lower sides of shell. Dimensions in Table 1.

Variation: Although fragments are common at Locality 9 and occur at 2 other localities along the Rio Grande Valley (see METCALF, 1967: 49), complete specimens were difficult to obtain and shells broke easily with handling. In the few specimens seen, the parietal tooth varied from the low swelling seen in the holotype to a condition where it was barely discernible. The basal tooth varied from a single low swelling (Figure *11* – a paratype) to the slightly higher, bifid condition seen in the holotype (Figure *12*). A barely discernible swelling in the outer lip of some specimens may be homologous to a palatal tooth.

Comparisons: This full-whorled, weakly denticulate species seems to resemble members of the *Ashmunella pseudodonta* (Dall, 1897) and *A. organensis* Pilsbry, 1936, complexes – both complexes highly variable with respect to size and degree of denticulation. *Ashmunella pseudodonta* was discussed above. *Ashmunella organensis* is found in the Organ Mountains, which border the Rio Grande Valley on the east and are, thus, not far removed geographically from the localities in which *A. hawleyi* occurs. If, as hypothesized by Pilsbry (1905: 225), the ancestral stock of the genus *Ashmunella* was a tridentate form, it is of interest that in at least one line a trend towards tooth reduction seems already to have been well under way in the pre-Wisconsinan Pleistocene (see discussion of age below).

Members of the genus *Ashmunella* in New Mexico are, at present, montane species. The ability of *A. hawleyi* to exist on the floodplain of the ancient Rio Grande suggests conditions much more favorable to the genus than exist along the river today. That an *Ashmunella* could tolerate the floodplain habitat at 4000 feet (1219 m) elevation suggests enhanced possibilities for genetic interchange between populations at that time, which are no longer possible with species restricted to isolated mountain masses.

Locality: (No. 10). Doña Ana Canyon, SW-¼, SW-¼, NW-¼, Sec. 22, T. 18 S, R. 4 W. 4090 feet (1247 m) elevation. Shells occur in sediments exposed in scarps below the Tortugas geomorphic surface, 2.3 miles (3.7 km) SE of Garfield on U. S. Highway 85 and then ⅛ mile (180 m) NE of the highway. **Type Locality** is in walls of first "valley" in the scarp, south of the point where a farm road (⅛ mile NE of its junction with U. S. Highway 85) turns sharply to the north, to parallel the base of the scarp.

Holotype: ANSP 325527; **Paratype:** ANSP 325526.

Etymology: The epithet honors Dr. John W. Hawley, in recognition of his valuable studies on Pleistocene geology of the middle Rio Grande region.

AGE

The Tortugas alluvium in which *Ashmunella hawleyi* occurs was discussed by Hawley (1965: 192) and Metcalf (1967: 21 - 25) with the latter suggesting an Illinoian age for sediments of the alluvium.

Judging by the ancient appearance (induration, cementation, surficial petrocalcic horizons) and subsequent large-scale dissection of the massive valley-fill units in which *Ashmunella ruidosana* and *A. jamesensis* and some populations of *A. tegillum* (Locality No. 7) occur, it seems that they surely date to a pre-Wisconsinan time of the Pleistocene. Perhaps these fill units are equivalent time-wise to the widespread and massive Tortugas alluvium of the Rio Grande Valley mentioned above. If this were the case, then that time (Illinoian?) would seem to have been especially favorable to extension of range of a number of *Ashmunella* (and of *Oreohelix*), allowing them to exist in places where they presently do not occur.

Some of the specimens of *Ashmunella tegillum* occur in a more recent colluvial material (Localities 6 and 8), probably of Wisconsinan age, suggesting that this species inhabited the Sacramento Mountains for a relatively long period of time.

The rocky colluvium containing *Ashmunella tularosana* seems to reflect conditions associated with a colder time, probably an Illinoian or Wisconsinan glaciation.

RELATIONSHIPS OF EASTERN ASHMUNELLAS

In working with the diverse species of *Ashmunella* in the Chiricahua and Huachuca Mountains of southeastern Arizona, Pilsbry (1940: 949, 964) concluded that the species of each range were more closely related *inter se* than to any species from another range, despite any superficial similarities. A similar diversity of species seems to have occupied the Sacramento Mountains at one time or another in the past. In this case, lack of knowledge of soft anatomy hampers phylogenetic interpretation. Nevertheless, the question may be considered whether this diversity is also to be attributed to radiation within a closely allied species group or whether the species were of diverse ancestries (within the genus). I take the view below that not one but several groups have been involved.

Of extant and fossil species of *Ashmunella* from the Rio Grande Valley eastward, three, and possibly four, groups might be discerned:

(1) *Ashmunella rhyssa* complex. This comprises 2 or more species or subspecies, or both, in the Sacramento-Sierra Blanca Mountains (and nearby mountains) (Edward M. Stern, 1970. Revision of the land snail genus *Ashmunella*: Sierra Blanca-Sacramento Mountains, New Mexico. Unpublished Master's Thesis, University of Texas at El Paso). An abundance of fossils of the *A. rhyssa* complex occurring throughout the Sacramento Mountains indicates that this has been the dominant group in the range as far back as the record is discernible. None of the fossils described above seem, however, to be closely allied

to the *A. rhyssa* group. Other fossils indicate that at least 2 well-defined races did arise from the *A. rhyssa* stock at times in the Pleistocene. Possibly these were localized races that were later "swamped" out. In any event they are no longer extant.

(2) *Ashmunella ruidosana* complex. Several species in the area east of the Rio Grande Valley have a generally similar shell morphology and exhibit a presumed advance over the hypothetical tridentate condition in that the basal tooth is (1) bifid, (2) has separated slightly into 2 distinct denticles, or (3) has become obsolescent. These species include *A. ruidosana, A. thomsoniana, A. pseudodonta, A. hawleyi,* and *A. organensis,* all mentioned above. Assuming that this group ancestrally had well-developed denticles, *A. ruidosana* might serve as an exemplar of this ancestral condition. *Ashmunella organensis* and *A. hawleyi,* on the other hand, would seem to have progressed farthest in regard to tooth reduction.

As *Ashmunella thomsoniana* is geographically a northern outlier of the genus, it seems reasonable to suppose that its original source area was to the south. This places the Sacramento-Sierra Blanca-Capitan Mountains (see Map) in a likely position as this source area and lends credence to the view that the ancestral stock of *A. thomsoniana* may have been close to *A. ruidosana.* Possibly the *A. pseudodonta* complex of the Capitan-Patos-Carrizo Mountains descended from this same ancestral stock. However, *A. pseudodonta* has suffered greater reduction of denticles than has *A. thomsoniana.*

It must be cautioned that the species considered in this group are widespread geographically and the resemblances in shell morphology may merely be reflecting convergencies that occurred independently in different mountain ranges rather than indicating relationships.

(3) *Ashmunella mearnsi* group. (Usage of Pilsbry, 1940: 972). This group ranges both east and west of the Rio Grande Valley. In the *A. mearnsi* group, the ancestral single basal tooth has evolved beyond the bifid condition seen in the preceding group and now comprises 2 distinct and relatively widely separated denticles in the lower lip. In most species of the *A. mearnsi* group, a second parietal tooth occurs in a position above that occupied by the parietal tooth observed in the preceding group. A further stage in the evolution of the parietal tooth into a complex shelflike structure is exemplified by *A. pasonis* (Drake, 1951) of the Franklin Mountains, Texas.

Ashmunella jamesensis and *A. tegillum* seem characteristically to have 2 parietal teeth. However, in one population (Locality **8**) of *A. tegillum,* the upper parietal is generally absent, perhaps because these are dwarfed, paedomorphic specimens, exhibiting an ontogenetically arrested condition that simulates to some extent an ancestral morphology predating evolution of the upper tooth.

The *Ashmunella mearnsi* group seems to have been especially successful in invading and colonizing many of the lower, more arid mountains of southern New Mexico and adjacent areas (see Map). However, presence of 2 representatives of the group as fossils in the Sacramento Mountains indicates that the group is relatively ancient. It is puzzling why both species have become extinct.

(4) In the account of *Ashmunella tularosana,* above, a relationship to the *A. tetrodon* group was postulated. In this view, *A. tularosana* would represent a colonization derived from a source west of the Rio Grande Valley. Alternatively, *A. tularosana* might be visualized as having evolved in the Sacramento Mountains from an ancestor similar to *A. ruidosana.* This would, however, have involved a rather marked depression in shell form and the evolution of the bifid basal tooth into 2 distinct, large, relatively widely separated teeth.

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The Northwest American Psammobiidae

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(4 Plates; 8 Text figures)

INTRODUCTION

This is the third article based on research conducted while I was a graduate student at Stanford University, the Tellinidae and Semelidae having been discussed in earlier papers (Coan, 1971, 1973). The main purpose of the present account is to put on record data on the systematics of the northwest American Psammobiidae. The present survey also permitted the review of data on the geographic and geologic distributions and habitats of members of this family. These aspects are summarized at the end of the article.

The major previous accounts on this family in northwestern America were those of Dall (1898), Grant & Gale (1931), and Burch (1945a-1945b).

The detailed "Introduction," "Acknowledgments," and "Methods" sections of my earlier paper need not be repeated here, although special thanks are extended to Drs. Myra Keen, Warren Addicott, and Kenneth Boss who reviewed the present manuscript, and to Mr. Barry Roth who prepared the illustrations. The following abridged comments on format and abbreviations will permit the present paper to stand alone.

(1) The applicable synonymous species-level names are listed in chronological order, with the name to be used cited first and "first revisions," if any, indicated. Under each name are listed accounts published using those names and also accounts of type material pertinent to each. These works are listed in chronological order with major changes in generic allocation indicated in brackets above the account in which they were first employed. It is to be assumed that nearly all subsequent accounts used the same name combination. Other nomenclatural comments are included in brackets after the account to which they refer.

The works listed do not represent a complete catalogue of literature but are the major accounts concerning living and fossil northwest American material, particularly those containing previously unpublished information or taxonomic innovations. Not included are books written largely for amateurs or general works on marine biology.

Numbers following dates (as 1851: 27) are page numbers.

(2) The type material pertinent to the valid name and its synonyms is discussed. Measurements given are of the greatest lengths of type specimens. When type material is no longer extant the dimensions from original accounts or of original illustrations are given. (In most early accounts the illustrations were usually printed at natural size, though this was rarely stated.) Photographs of type specimens or of original illustrations are included.

(3) Type localities of the various nominal species are given. The original collector is also cited, and sometimes major collections are mentioned when this clarifies the history or location of the specimens.

(4) A nomenclatural commentary may be given to explain nomenclatural complications not made clear in the synonymy or in the discussion of type material.

(5) Description. A short diagnosis of each species is given that emphasizes distinguishing characters. Most features of internal shell morphology are not discussed in detail but are illustrated with line drawings.

(6) Geographic Distribution and Ecology. The end-points of the distribution are given, together with reference to the sources of the records. The intermediate distributional data from between these end-points are summarized.

The sources of habitat information on each species other than from museum labels are indicated. I mention also the approximate number of lots examined.

(7) Geologic Distribution and Biogeography. The final section under each species is a summary of paleontologic

records from published accounts. I have not listed all Pleistocene records, but generally have given only the end-points of their distributions and indicated the published accounts that form their bases. This is followed by notes on earlier records, on what seem to be related west American fossil species from earlier than the Pleistocene and other related species in other provinces.

References are included under "Literature Cited" for all genera, species, and papers mentioned.

Conventions, symbols, and abbreviations used are as follows:

AMNH – American Museum of Natural History, New York, New York
ANSP – Academy of Natural Sciences, Philadelphia, Pennsylvania
BM(NH) – British Museum (Natural History), London, England
CAS – California Academy of Sciences, San Francisco, California
cm – centimeter(s)
ex (Conrad) MS – from the manuscript name of (Conrad)
ICZN – International Commission on Zoological Nomenclature, or International Code of Zoological Nomenclature (Stoll *et al.*, 1964)
"in synonymy" – a name proposed in the synonymy of another and therefore not available
LACM – Los Angeles County Museum of Natural History, Los Angeles, California
m – meter(s)
MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
mm – millimeter(s)
nomen nudum – an unavailable name lacking any description, definition, or other indication
not, not of – as in the case of homonyms or misidentifications
pair – the two valves of one specimen
SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, California
SDNHM – San Diego Natural History Museum, San Diego, California
SU – Stanford University, Stanford, California
UCB – University of California at Berkeley, California
UCD – University of California at Davis, California
USNM – United States National Museum, Smithsonian Institution, Washington, District of Columbia

SYSTEMATIC ACCOUNT

Psammobiidae Fleming, 1828

[Name retained: ICZN (1970), Opinion 910]

Keen (1969) recognized both the family Psammobiidae and the family Solecurtidae. Here I adopt a more conservative approach, regarding the latter as a subfamily. A comprehensive analysis of the familial and generic classification of these groups should be undertaken.

There are a number of accounts on the anatomy and functional morphology of members of this family. These studies have been conducted for the most part on species not from west America, and it is beyond the scope of the present paper to review them in detail.

Among the Psammobiinae, European species of the genus *Gari* are discussed by Bloomer (1911), Yonge (1949), Purchon (1960), and Ansell (1967); these authors review still earlier papers. The genus *Asaphis* has been described by White (1942) and Purchon (1960).

In the Sanguinolariinae, a single species of *Sanguinolaria* is discussed by Dinamani (1967).

The Solecurtinae seems to be the best known of subfamilies of the Psammobiidae. Relevant papers, containing references to still other accounts, are Ghosh (1920), White (1942), Yonge (1949, 1952), Purchon (1960), and Jegla & Greenberg (1968).

Psammobiinae Fleming, 1828

Into the Psammobiinae are placed those members of the Psammobiidae that are elongate to ovate-elongate and are not conspicuously inequivalve. Many are sculptured, and the gape is small to absent. Pallial sinuses tend to be smaller than those in the Sanguinolariinae.

Gari Schumacher, 1817

[Type species: *Gari vulgaris* Schumacher, 1817, by ICZN (1970), Opinion 910, =*Solen amethystus* Wood, 1815]

The genus *Gari* contains most species of living Psammobiinae. Their shells are elongate-ovate to quadrate and are smooth to well sculptured. The posterior end is often wider than the anterior and is more or less truncate.

(Gobraeus) Brown, 1844, *ex* Leach MS

[Published in synonymy; name retained under ICZN Article 11(b). Type species: *Solen vespertinus* Gmelin, 1791, by M, = *Tellina depressa* Pennant, 1777]

The subgenus *Gobraeus* is characterized by species whose shells are nearly smooth or have concentric sculpture of growth lines only (the posterior slope may also have some fine superficial radial striae). The pallial sinus is partly confluent with the pallial line. Many species attain a large size.

Hertlein & Grant (1972) regarded *Gobraeus* as a full genus. I remain conservative in this matter until a more thorough review of generic units in the *Gari* complex is undertaken. It is unclear, for instance, how closely the type species of *Gobraeus* is related to west American species.

Gari (Gobraeus) californica (Conrad, 1849)

(Figures *1* and 20)

Psammobia californica Conrad
- [Conrad, 1837: plt. 19, fig. 3 (figure only, not validated)]
- Conrad, 1849: 121 [based on the above figure]
- Carpenter, 1864c: 633 [1872: 119]

[*Psammobia (Gobraeus)*]
- Dall, 1898: 58
- I. Oldroyd, 1924: 57, 215; plt. 46, fig. 3
- I. Oldroyd, 1925: 185; plt. 43, fig. 5

[*Gari (Gobraeus)*]
- Grant & Gale, 1931: 382
- Burch, 1945a: 21-22, 26 (text fig.); 1945b: 17

"*Sanguinolaria rubro-radiata* Conrad," Carpenter, *ex* Nuttall MS [*nomen nudum*]
- Carpenter, 1857a: 212
- Carpenter, 1857b: 195, 301
- Carpenter, 1860: 1

Psammobia rubroradiata Carpenter, *ex* Nuttall MS [*rubrolineata*, misspelling of authors]
- Carpenter, 1864c: 540, 563, 602, 638 [1872: 26, 49, 88, 124]
- Carpenter, 1865: 55
- Dall, 1898: 61 [as a synonym of *P. californica*]
- Palmer, 1958: 17, 20, 112-113, 341; plt. 16, figs. 3-5, 7

Psammobia lilacina Wilkins, in Palmer, *ex* Carpenter MS [in synonymy]
- Palmer, 1958: 113

Type Material:

Psammobia californica & *P. rubroradiata* – BM(NH) Nuttall collection 1861.5.20.88, pair, 41.2 mm. This is the holotype of Conrad's species and a lectotype (Palmer, 1958) of Carpenter's. Evidently, neither Carpenter nor Palmer were aware that this specimen was also Conrad's type specimen. Figure *1*.

Type Locality:

Psammobia californica & *P. rubroradiata* – None given by Conrad (1837, 1849), but presumably from California; T. Nuttall.

Nomenclatural Commentary:

None necessary.

Description:

Large (to 115 mm); quadrate; heavy; anterior end rounded; longer, broadly truncate posteriorly; beaks relatively prominent, dorsal margins sloping from them more abruptly than in other species; sculpture of irregular concentric undulations; periostracum tan, lost relatively early and present only as ventral shreds in adult; externally rayed with reddish lines. Internal details shown in Figure 20.

Geographic Distribution and Ecology:

Shelikof Strait, Alaska (USNM 207429); southwestern end of Prince William Sound, Alaska (CAS 42150, 48868; Talmadge and Baxter, *in litt.*), to Neah Bay, Washington (USNM 15636), with many intermediate records; Mendocino County, California (UCB 3094), to Bahía Magdalena, Baja California Sur (ANSP 151756; CAS 20300; LACM material), with many intermediate records. Recent collections have not reconfirmed its presence west of Prince William Sound (Baxter, *in litt.*). Records from the Pacific coasts of Oregon and Washington are lacking. This species is found from the intertidal area to 168 m, among rubble; also buried to a depth of 20 cm in finer sediments near bay entrances (Burch, 1945a; Fitch, 1953; Talmadge, *in litt.*) and offshore (Smith & Gordon, 1948).

Material seen:

164 lots.

Explanation of Figures *1* to *4*

Figure *1*: *Gari (Gobraeus) californica*. Holotype of *Psammobia californica* and lectotype of *Psammobia rubroradiata*, BM(NH), Nuttall collection 1861.5.20.88; 41.2 mm

Figure *2*: *Gari (Gobraeus) edentula*. Holotype of *Siliquaria edentula*, MCZ (Palaeontology) 15035; 66 mm

Figure *3*: Holotype of *Tellina fucata*. BM(NH) 79.2.26.192; 41 mm

Figure *4*: *Gari (Gobraeus) edentula*, juvenile, USNM 152745, San Pedro, California, 18 m; 28.4 mm

Figure *1*

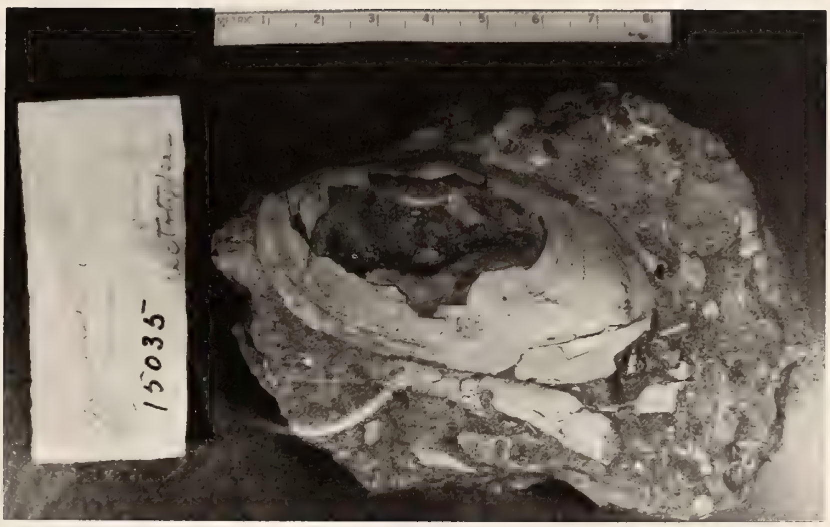

Figure *2*

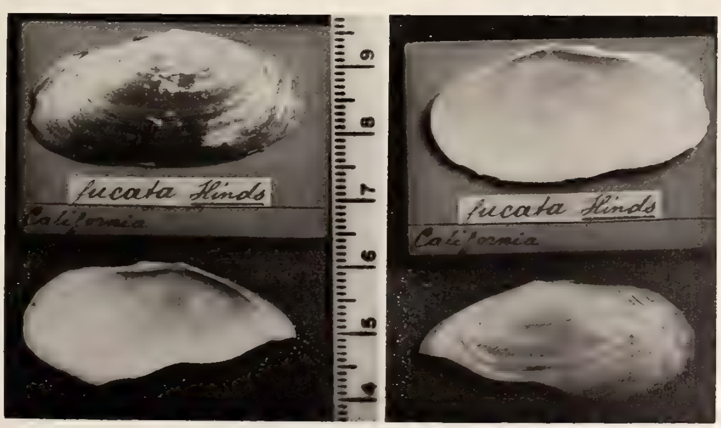

Figure *3*

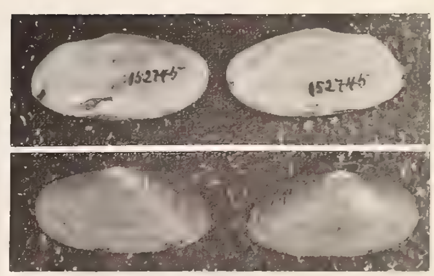

Figure *4*

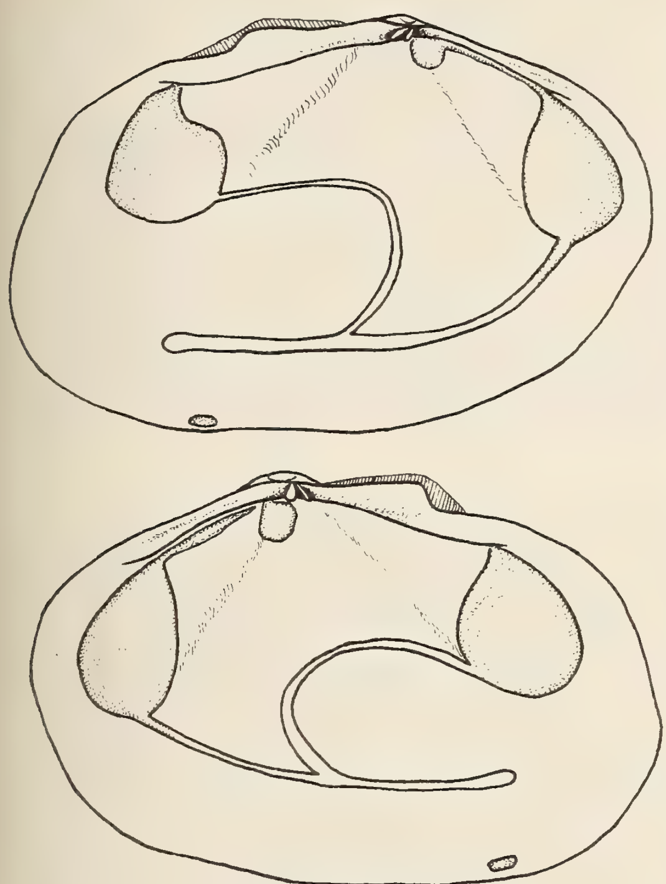

Figure 20

Gari (Gobraeus) californica

Internal view of valves
MCZ 67244, San Diego, California; 107 mm

Geologic Distribution and Biogeography:

Gari californica has been reported in the late Pleistocene from San Nicholas Island (Vedder & Norris, 1963) to San Diego (Emerson & Addicott, 1953; Valentine, 1961; Bishop & Bishop, 1972), California. It is also known in the early Pleistocene from the Santa Monica area (Hoots, 1931; Rodda, 1957) to the San Pedro area (T. Oldroyd, 1925; Burch, 1947; Clark, *in* Natland, 1957; Valentine & Meade, 1961), California. There are two records in the Pliocene of southern California, but there do not seem to be related fossil species in the eastern Pacific.

There is a homologous species in Japan, *Gari (Gobraeus) kazusensis* (Yokoyama, 1922), which is said to lack radial rays and to be more truncate posteriorly (Kira, 1962). However, material in the USNM does not convincingly confirm these differences; additional material should be studied to provide a more detailed comparison. There is a wide geographic separation between the two species.

Other related members of this subgenus occur in the Panamic province (Keen, 1971), but none seems as close as *Gari kazusensis.*

Gari (Gobraeus) edentula (Gabb, 1869)

(Figures *2* to *5* and 21)

Siliquaria edentula Gabb
Gabb, 1869: 53, 89; plt. 15, fig. 11 [generic placement questioned by Gabb]

[*Psammobia (Gobraeus)*]
Dall, 1898: 58, 61

[*Psammobia (Psammobia)*]
Arnold, 1903: 168

[*Psammobia (Gobraeus)*]
Dall, 1925: 23, 37; plt. 19, fig. 1
I. Oldroyd, 1925: 185; plt. 57, fig. 1

[*Gari*]
Stewart, 1930: 7, 281 - 282; plt. 13, fig. 3

[*Gari (Gobraeus)*]
Grant & Gale, 1931: 382, 924; plt. 21, fig. 5
Burch, 1945a: 22; 1945b: 18

[*Gobraeus*]
Hertlein & Grant, 1972: 305; plt. 48, figs. 13, 15

?*Tellina fucata* Hinds
Hinds, 1845: 67; plt. 21, fig. 4
Carpenter, 1857b: 207

[*Psammobia (Gobraeus)*]
Dall, 1898: 58, 62

[*Gari*]
Olsson, 1961: 357
Palmer, 1963: 313
Keen, 1966b: 268; plt. 46, fig. 4
Keen, 1971: 240 - 241; fig. 602

Type Material:

Siliquaria edentula – MCZ (Paleontology) 15035, holotype, left valve, 66 mm. Figure *2*.

Tellina fucata – BM(NH) 79.2.26.192, holotype, pair, 41 mm. Figure *3*.

Type Localities:

Siliquaria edentula – San Fernando, Los Angeles County, California; Pliocene.

Tellina fucata – Bahía Magdalena, Baja California Sur; R. B. Hinds.

Nomenclatural Commentary:

Hind's *Tellina fucata* may be an earlier name for the offshore southern Californian species *Gari edentula*. The type specimen of Hind's species is very similar to young specimens from California (Figure *4*). However, this species is not known as an adult from Bahía Magdalena. Indeed, the species is not known from south of Catalina Island, southern California, but it is also possible that Hind's specimen was actually from farther north. Thus, it seems that a name change may be in order when more data are available.

Description:

Large (to 140 mm); ovate-elongate; relatively thin and flat for size; rounded, slightly pointed anteriorly; broadly truncate posteriorly; beaks proportionately small; dorsal margin relatively straight; sculpture of weak concentric lines; periostracum olive-tan; surface rayed with dark lines (Figure *5*). Internal details shown in Figure 21.

Geographic Distribution and Ecology:

Vicinity of Santa Barbara (Fitch, 1953 & *in litt.*) to San Pedro (USNM 568679 and other lots in various collections) and Catalina Island (USNM 107774), California; ?San Diego, California (Fitch, 1953; I have seen no specimens); possibly to Bahía Magdalena, Baja California Sur (type locality of *Tellina fucata*). This species has been taken from 5 to 137 m, buried in about 15 cm in fine sand (Fitch, 1953).

Material seen:

31 lots

Geologic Distribution and Biogeography:

Gari edentula is known from the late Pleistocene from Point Dume (Addicott, 1964) to Newport Bay (Kanakoff & Emerson, 1959), California. In the early Pleistocene it has been recorded from the northwestern end of the Los Angeles basin (Rodda, 1957) and San Pedro (De Long, 1941; Valentine & Meade, 1961). It has been reported in Californian formations transitional between the Pleistocene and Pliocene and from the Pliocene of southern California and northwestern Baja California. There is one uncertain Miocene record.

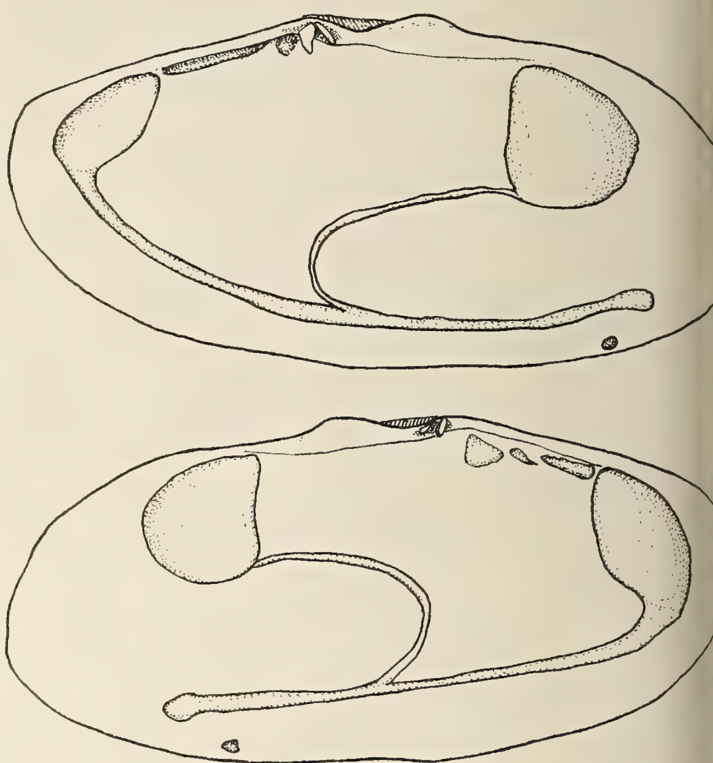

Figure 21

Gari (Gobraeus) edentula

Internal view of valves
MCZ 210459, San Pedro, California; 123 mm

Explanation of Figures 5 to 9

Figure *5*: *Gari (Gobraeus) edentula*. CAS 13320, San Pedro, California; 125 mm

Figure *6*: *Gari (Gobraeus) regularis*. Holotype of *Psammobia (?Amphichaena) regularis*, USNM 19407; 26.7 mm

Figure *7*: *Gari (Gobraeus) regularis*. USNM 207676, U. S. Fish Commission station 2932, Islas Los Coronados, Baja California Norte, 37 m; 24 mm

Figure *8*: *Heterodonax pacificus*. Lectotype (herein) of *Psammobia pacifica*, BM(NH) Nuttall collection 1861.5.20.93; 24.5 mm

Figure *9*: *Heterodonax bimaculatus* (Linnaeus, 1758). Potential lectotype (uppermost specimen) and paralectotypes (below) of *Tellina bimaculata*, Linnean Society of London; potential lectotype measures 13.5 mm

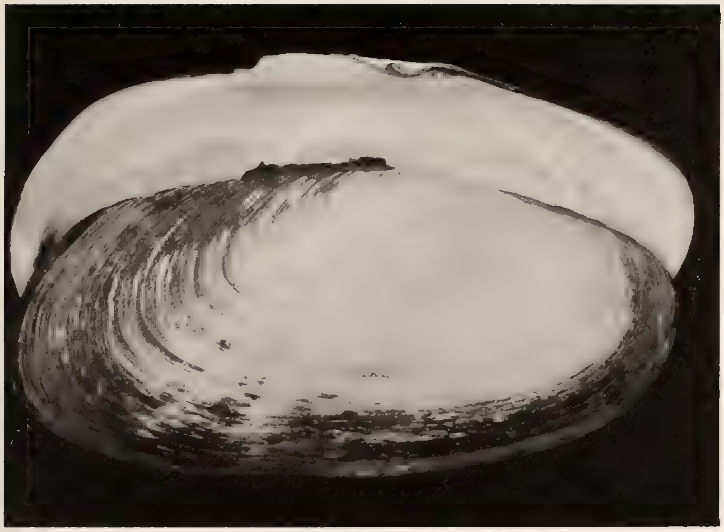

Figure 5

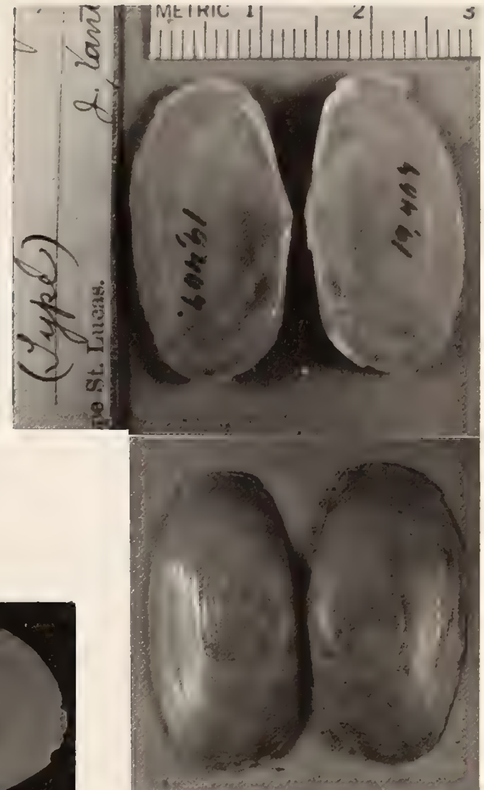

Figure 6

Figure 7

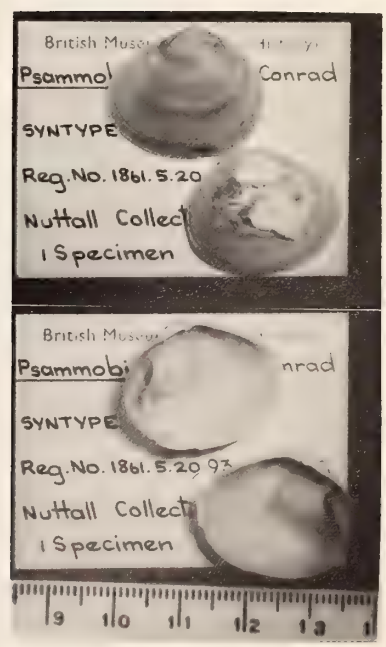

Figure 8

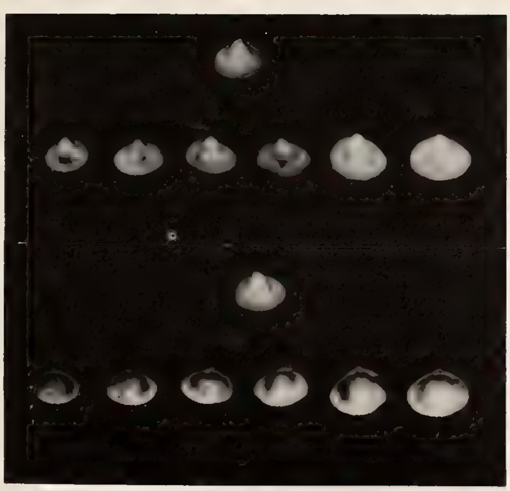

Figure 9

This species might be compared with *Gari martini* (Dickerson, 1917) from the Oligocene of southwestern Washington. I know of no related Asian species.

Gari (Gobraeus) regularis (Carpenter, 1864)

(Figures 6, 7, and 22)

Psammobia (?Amphichaena) regularis Carpenter, but not the *P. regularis* of some authors

CARPENTER, 1864b: 312 [1872: 210]
CARPENTER, 1864c: 618 [1872: 104]

[*Psammobia (Gobraeus)*

DALL, 1898: 57
I. OLDROYD, 1925: 184

[*Gari (Gobraeus)*]

BURCH, 1945a: 21; 1945b: 17
PALMER, 1958: 27, 44, 48, 113 - 114, 340; plt. 15, figs. 1 - 6
OLSSON, 1961: 356 - 357
PALMER, 1963: 313
KEEN, 1971: 242 - 243; fig. 608
[not KEEN, 1958: 190 - 191; fig. 466]

Type Material:
USNM 19407, holotype, pair, 26.7 mm. Figure 6.

Type Locality:
Cabo San Lucas, Baja California Sur; J. Xantus.

Nomenclatural Commentary:
This species, perhaps characteristic of the outer coast of Baja California, has been confused with an unrelated species in the Gulf of California, the latter now tentatively referred to *Gari helenae* Olsson, 1961 (KEEN, 1971).

Description:
Small (to 27 mm); elongate-ovate; flattened; thin; equilateral to slightly longer either anteriorly or posteriorly; sharply rounded anteriorly; somewhat truncate posteriorly; dorsal margins weakly sloping; externally with low growth striae and an adherent green periostracum which is somewhat roughened posteriorly; posterior slope with a light band. Internal details shown in Figure 22.

This species differs from young *Gari edentula* in having a lighter, more shiny periostracum which is less roughened posteriorly. The posterior slope is also less set off from the central slope.

Geographic Distribution and Ecology:
Off Islas Los Coronados, Baja California Norte (US NM 207676) (Figure 7), to Cabo San Lucas, Baja California Sur (type lot), with one other specimen from Isla Cedros, Baja California Norte (USNM 157944), tentatively referred to this species. The Islas Coronados specimen was taken in 37 m on a sand and shell bottom; the Isla Cedros specimen was taken in about 18 m.

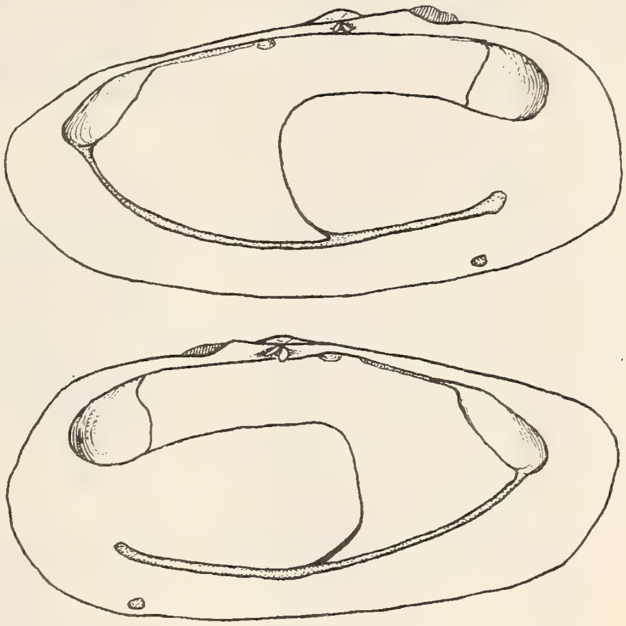

Figure 22

Gari (Gobraeus) regularis

Internal view of valves
USNM 207676, Islas Las Coronados, Baja California Norte; 24 mm

Material seen:
2 lots.

Geologic Distribution and Biogeography:
This rare species is not known as a fossil.

Heterodonax Mörch, 1853

[Type species: *Tellina bimaculata* Linnaeus, 1758, by SD of KOBELT, 1881]

This unique genus, about which little is known, is apparently restricted to the coasts of temperate and tropical America (KEEN, 1969). Its shell is rounded-quadrate, smooth except for concentric growth striae. The hinge teeth are proportionately large for the size of the adult specimen.

As common as is living material in southern California and northern Mexico, no anatomical study of this

genus has been made. This should be a priority project for an interested student.

Heterodonax pacificus (Conrad, 1837)

(Figures *8* to *13* and 23)

Psammobia pacifica Conrad
 CONRAD, 1837: 241; plt. 18, fig. 13

[*Sanguinolaria*]
 CARPENTER, 1857a: 212

[*Psammobia*]
 CARPENTER, 1857b: 195, 301, 351

[*Heterodonax*]
 CARPENTER, 1864c: 526, 552, 592, 640 [1872: 12, 38, 78, 126] [as a synonym of *H. bimaculatus*]
 KEEN, 1966a: 171
 KEEN, 1971: 242 - 243; fig. 609

Tellina bimaculata Linnaeus, of authors, not of Linnaeus
 [not Linnaeus, 1758: 677]

[*Heterodonax*]
 CARPENTER, 1864c: 526, 537, 541, 619, 626, 640, 665 [1872: 12, 23, 27, 78, 105, 126, 151]
 DALL, 1900: 980
 I. OLDROYD, 1925: 186
 BURCH, 1945a: 22, 24 (text fig.); 1945b: 18
 HERTLEIN & STRONG, 1950: 221 - 222
 KEEN, 1958: 190 - 191; fig. 467
 OLSSON, 1961: 354 - 355, 558; plt. 85, fig. 10

Tellina vicina C. B. Adams
 ADAMS, 1852a: 509 - 510, 546 [ADAMS, 1852b: 285 - 286, 322]
 CARPENTER, 1857b: 232, 279, 284, 302, 351, 363

[*Heterodonax*]
 CARPENTER, 1864a: 367 [1872: 203]
 CARPENTER, 1864c: 526, 552, 592, 640 [1872: 12, 38, 78, 126] [as a synonym of *H. bimaculatus*]
 TURNER, 1956: 98, 128; plt. 18, figs. 11, 12

Donax ovalinus Reeve, *ex* Deshayes MS [as *D. "ovalina"*]
 REEVE, 1854: plt. 3, fig. 17
 DESHAYES, 1855: 352

[*Heterodonax*]
 HERTLEIN & STRONG, 1950: 221 [as a synonym of *H. bimaculatus*]

Tellina versicolor Carpenter, *ex* C. B. Adams MS, not of DEKAY [in synonymy]
 [not DEKAY, 1843, *ex* COZZENS MS: 209; plt. 26, fig. 172]
 CARPENTER, 1864a: 29 [1872: 203]
 CARPENTER, 1864c: 552 [1872: 38]

Heterodonax bimaculatus purpureus Williamson
 WILLIAMSON, 1892: 187

Heterodonax bimaculatus salmoneus Williamson
 WILLIAMSON, 1892: 187

Type Material:

Psammobia pacifica – BM(NH) Nuttall collection 1861.5.20.93, **lectotype** herein, pair, 24.5 mm, possibly the specimen figured by CONRAD (1837); BM (NH) Nuttall collection 1861.5.20.92, **paralectotype**, pair. Figure *8*.

Tellina bimaculata (not a synonym) – Linnean Society of London, potential lectotype, the unseparated pair, 13.5 mm; potential paralectotypes, 6 valves. It is to be hoped that what appear to be lateral teeth in the right valves of this lot are in reality especially heavy ligamental buttresses. Otherwise some serious nomenclatural problems would result! Figure *9*.

Tellina vicina – MCZ 186365, lectotype (TURNER, 1956), pair, 20.9 mm; MCZ 186369, paralectotypes, 4 pairs. Figure *10*.

Donax ovalinus – BM(NH) without registry number, **lectotype** herein, the larger of two pairs, about 30 mm; **paralectotype**, the other pair. Figure *11*.

Heterodonax bimaculatus purpureus – LACM 1168, **lectotype** herein, pair, 27.5 mm; LACM 1176, **paralectotypes**, 8 pairs, 2 valves. Figure *12*.

Explanation of Figures *10* to *15*

Figure *10*: *Heterodonax pacificus*. Lectotype of *Tellina vicina*, MCZ 186365; 20.9 mm
Figure *11*: *Heterodonax pacificus*. Lectotype (herein) of *Donax ovalinus*, BM(NH) without registry number; about 30 mm
Figure *12*: *Heterodonax pacificus*. Lectotype (herein) of *Heterodonax bimaculatus purpureus*, LACM 1168; 27.5 mm
Figure *13*: *Heterodonax pacificus*. Lectotype (herein) of *Heterodonax bimaculatus salmoneus*, LACM 1169; 15.6 mm
Figure *14*: *Nuttallia nuttallii*. Lectotype (herein) of *Sanguinolaria nuttallii*, BM(NH) Nuttall collection 1966.302; 56 mm
Figure *15*: *Nuttallia nuttallii*. Original illustration of *Psammobia decora*; 71 mm (HINDS, 1842)

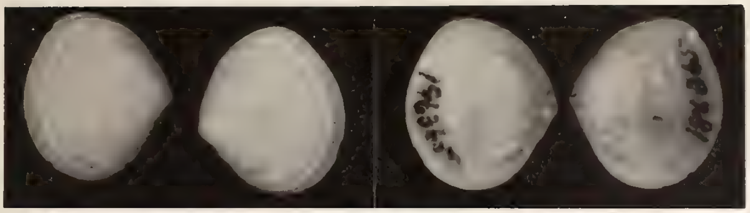

Figure *10*

Figure *11*

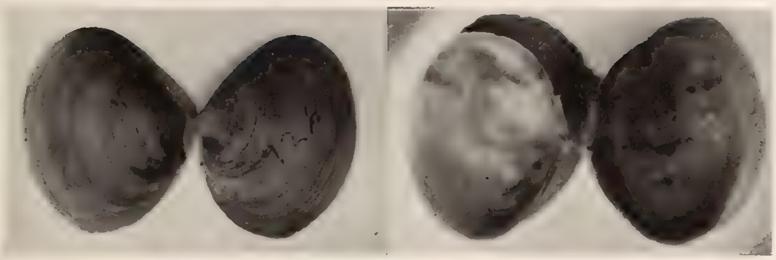

Figure *12*

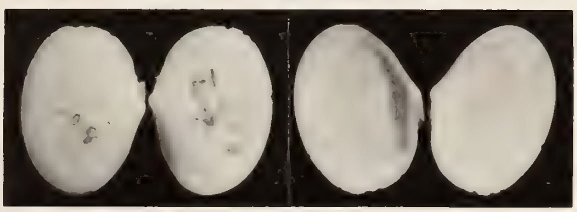

Figure *13*

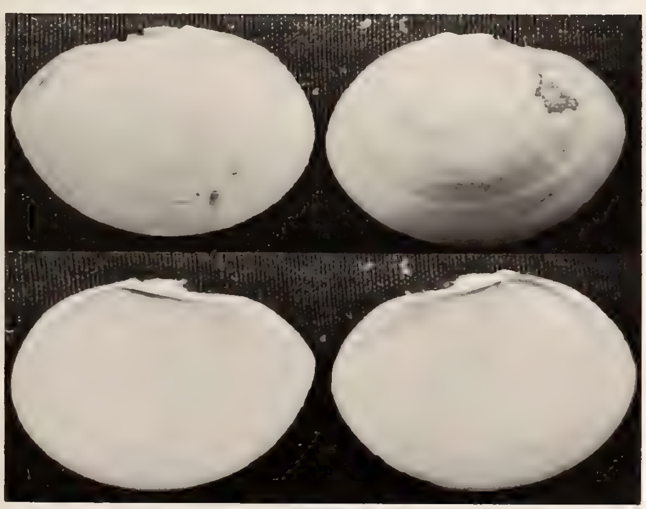

Figure *14*

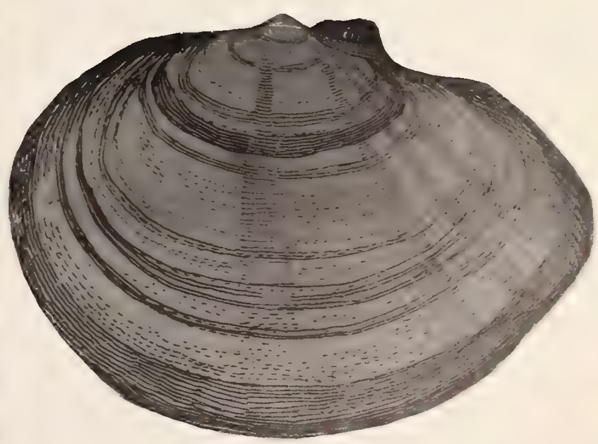

Figure *15*

Heterodonax bimaculatus salmoneus – LACM 1169, lectotype herein, 15.6mm; LACM 1177, paralectotypes, 1 pair, 21 valves. Figure *13*.

Type Localities:

Psammobia pacifica – "near" San Diego, California; T. Nuttall, "in deepish water" on a sandy bottom.

Tellina bimaculata – "European Ocean," in error. It is from the Caribbean.

Tellina vicina – West coast of Panama; C. B. Adams.

Donax ovalinus – Central America; H. Cuming.

Heterodonax bimaculatus purpureus and *H. b. salmoneus* – San Pedro, California; M. B. Williamson.

Nomenclatural Commentary:

Following Coan, *in* Keen (1971), the Pacific and Atlantic forms are regarded as separate species, *Heterodonax pacificus* being larger and having a pallial sinus that tends to approach the pallial line at a right angle, but not to meet it (Figure 23). In *H. bimaculatus* the pallial sinus tends to merge with the pallial line at an angle.

Panamic material, particularly from the southern end of its distribution, tends to be thicker than specimens from California (Dr. S. S. Berry, verbal communication). After careful statistical study of specimens from Mexico and Central America workers may choose to regard all or part of this material as representing a subspecies, *Heterodonax pacificus vicinus*.

Description:

Large for genus (to 30mm); oval; equivalve; longer, rounded anteriorly; weakly to well truncate posteriorly; sculpture of rounded, concentric ribs, occasionally with a few radial grooves; externally white, purple, pink, or orange, occasionally with dark flecks, rays, or blotches; similarly colored internally; pallial sinuses striose. Other internal details shown in Figure 23.

Geographic Distribution and Ecology:

Point Conception, California (SU 4696), through southern California and the entire Panamic province to Tumbez, Peru (Olsson, 1961), with many intermediate records. More northerly records from Monterey, California (UCB 2395; Smith & Gordon, 1948) may represent larval settlements in especially warm years or errors in labeling. Specimens labeled as having come from the "Columbia River" (ANSP 51617; AMNH 33580 & 33-581) are most certainly in error. *Heterodonax pacificus* is found intertidally in protected bays in sand, relatively close to the surface (Burch, 1945a).

Material seen:

93 lots from area of study.

Geologic Distribution and Biogeography:

This species is known as a west American fossil only

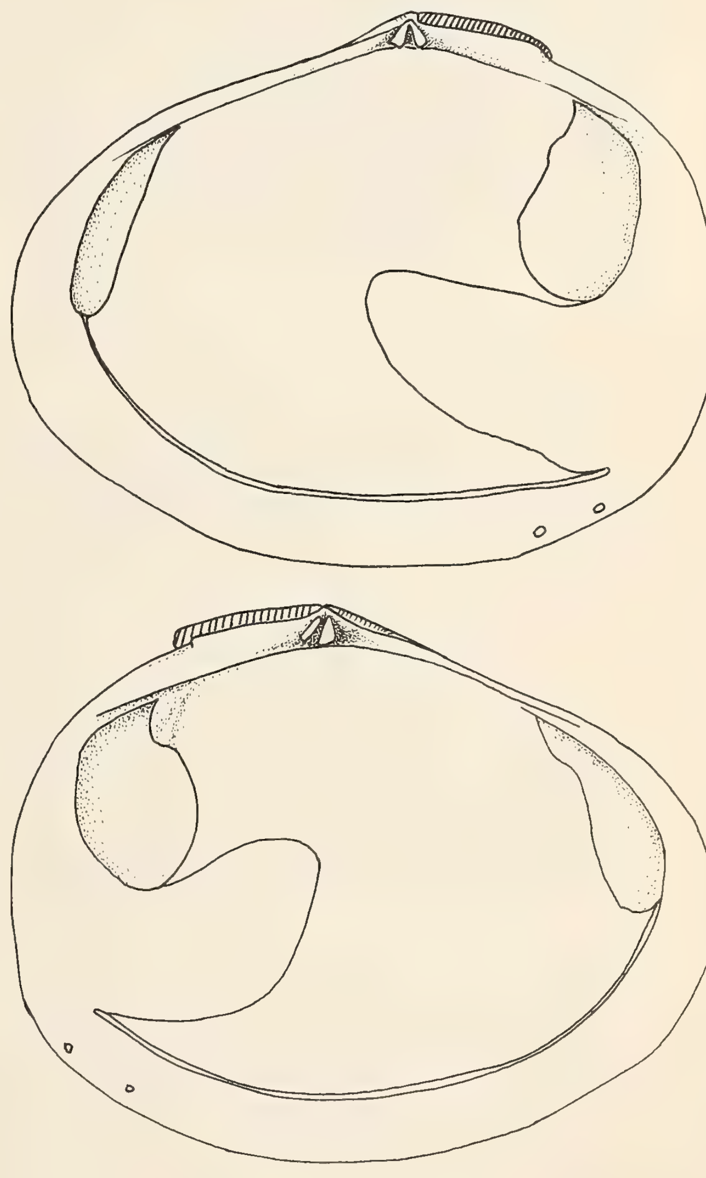

Figure 23

Heterodonax pacificus

Internal view of valves

SU 148/1, San Diego, California; 25.4 mm

from the late Pleistocene of the San Pedro area, California (DALL, 1900), to Bahía Magdalena, Baja California Sur (JORDAN, 1936), with two intermediate records. It appears to have been a late arrival in the Californian province, having been derived from the Caribbean homologue, *Heterodonax bimaculatus*.

Sanguinolariinae Grant & Gale, 1931

Into this subfamily are placed those members of the Psammobiidae that are elongate to ovate and are conspicuously inequivalve. They are mostly smooth, and may have a heavy, adherent periostracum. Pallial sinuses tend to be larger than those of the Psammobiinae. The gape is less conspicuous than in the Solecurtinae.

Nuttallia Dall, 1898

[Type species: *Sanguinolaria nuttallii* Conrad, 1837, by OD]

Following the recent practice of Japanese authors, the genus *Nuttallia* is here regarded as being distinct from *Sanguinolaria*. Species of *Nuttallia* are characteristically large, oval, with a much flattened right valve. A shiny, adherent periostracum is present.

Nuttallia nuttallii (Conrad, 1837)

(Figures *14* to *16* and 24)

Sanguinolaria nuttallii Conrad
CONRAD, 1837: 230 - 231; plt. 17, fig. 6
CONRAD, 1849: 214
CARPENTER, 1857a: 212
CARPENTER, 1857b: 195, 207, 226, 231, 234, 301, 351, 352
CARPENTER, 1864c: 540, 584, 588, 638, 665, 683 [1872: 26, 70, 74, 124, 151, 169]

[*Sanguinolaria (Nuttallia)*]
DALL, 1898: 58
ARNOLD, 1903: 168 - 169
I. OLDROYD, 1925: 185 - 186; plt. 55, figs. 1, 4
GRANT & GALE, 1931: 383; plt. 20, figs. 15a, 15b
BURCH, 1945a: 22, 24 (text fig.); 1945b: 18
KEEN, 1966a: 171

Psammobia decora Hinds
HINDS, 1842: 81; plt. 6, fig. 1
HINDS, 1845: 66 - 67; plt. 19, figs. 6, 7
CONRAD, 1849: 214 [as a synonym of *S. nuttallii*]
KEEN, 1966b: 268

Sanguinolaria grandis Carpenter, *ex* Gould MS [*nomen nudum*]
CARPENTER, 1857b: 228, 349

Sanguinolaria orcutti Dall
DALL, 1921: 17
DALL, 1925: 26, 36; plt. 12, figs. 1, 2
JORDAN, 1926: 224, 249 - 250; text fig. 1
GRANT & GALE, 1931: 383 - 384 [as a synonym of *S. nuttallii*]

Type Material:

Sanguinolaria nuttallii – BM(NH) Nuttall collection 1966.302, lectotype herein, the specimen with the less broken periostracum on left valve, pair, 56mm; paralectotype, pair, approximately same size. Figure *14*.

Psammobia decora. – Lost (KEEN, 1966b), 71mm (HINDS, 1842). Figure *15*.

Sanguinolaria orcutti – USNM 333118, holotype, pair, 130mm; USNM 645105, pair, figured by DALL (1925) but apparently received later than 1921. Figure *16*.

Type Localities:

Sanguinolaria nuttallii – San Diego, California; T. Nuttall, in marshes.

Psammobia decora – San Diego, California; R. B. Hinds.

Sanguinolaria orcutti – Bahía San Quintín, Baja California Norte; late Pleistocene [as "late Pliocene or early Pleistocene"]; C. R. Orcutt.

Nomenclatural Commentary:

GRANT & GALE (1931) found Dall's *Sanguinolaria orcutti* indistinguishable from *S. nuttallii,* and I concur in this opinion. The reported hinge differences seem not to be significant, and many molluscan species in the Pleistocene of Bahía San Quintín appear to have grown to a relatively large size. It must have been a favorable place to live.

Description:

Large for genus (to 150mm); ovate, longer posteriorly; left valve more inflated; thin; rounded anteriorly; broadly truncate dorso-posteriorly; smooth, except for concentric growth lines; covered with an adherent, light to dark brown, shiny periostracum; sometimes with dark, radial lines externally; purplish internally. Other internal details shown in Figure 24.

Geographic Distribution and Ecology:

Bodega Bay, California (UCD collection; STOHLER, 1959), to Bahía Magdalena, Baja California Sur (USNM 217818), with many intermediate localities. Specimens labeled as coming from Oaxaca, Mexico (SDNHM 18549), probably represent an error. This species is found in the intertidal area of protected bays, particularly near

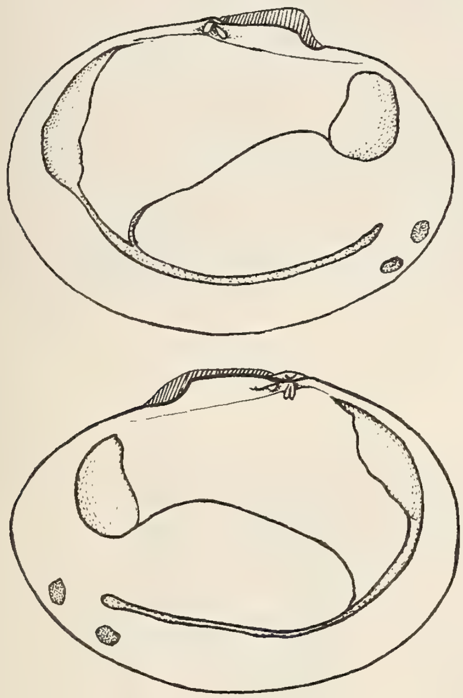

Figure 24

Nuttallia nuttallii

Internal view of valves
MCZ 140680, False Bay, San Diego, California; 74 mm

entrance channels, buried in sand or gravel to a depth of about 30 to 40 cm. They lie horizontally, with the convex left valve uppermost. They are uncommon in sand below the area of wave action on more open coast (WEYMOUTH, 1921; MACGINITIE, 1935; BURCH, 1945a; FITCH, 1953). POHLO (1972) describes the morphology of the soft parts and reports the species to be a non-selective suspension feeder.

Material seen:
121 lots.

Geologic Distribution and Biogeography:
Nuttallia nuttallii has been reported in the late Pleistocene from Summerland, California (VALENTINE, 1961) to Bahía Magdalena, Baja California Sur (JORDAN, 1936), with a number of intermediate records. There are two records in the early Pleistocene, both from the San Pedro area, California (T. OLDROYD, 1925; BURCH, 1947). It has also been reported in both the Pliocene and the Miocene of California.

Comparisons should be made to *Nuttallia alata* (Gabb, 1869) from the Miocene of California and to *N. toulai* (HERTLEIN & JORDAN, 1927) from the Miocene of Baja California Sur. Other species of the genus are reported from the Oligocene and Eocene of California.

There are apparently three Recent species of *Nuttallia* in Japan. The most similar of these is *N. ezonis* Kuroda & Habe, *in* HABE, 1955. The Californian species differs in being larger, broader posteriorly, and in having a longer pallial sinus. The periostracum of *N. nuttallii* is also thinner and lighter in color.

Solecurtinae d'Orbigny, 1846

This subfamily is composed of those members of the Psammobiidae that are elongate, equivalve, and widely gaping at both ends. Most are smooth or have a few incised oblique lines. The periostracum may be adherent or easily worn off.

Tagelus Gray, 1847

[Type species: *"Sol. guinensis"*, by OD of Gray, 1847, = *Solen guineensis* Holten, 1802, *ex* Chemnitz MS (not to be confused with *Solen guinensis* Hanley, 1842, *ex* Gray MS, a member of the Solenidae), =*Solen adansonii* Bosc, 1801 (better known as *Solecurtus angulatus* Sowerby, 1874), an African species regarded by some authors as being the same as *Solen plebeius* [Lightfoot], 1786, a Caribbean species. The two species are probably distinct.]

Members of the genus *Tagelus* are smooth, elongate, and more or less equilateral. The anatomies of a number of species have been described (BLOOMER, 1903a, 1903b; 1905; 1907a, 1907b; HOFFMANN, 1914; GHOSH, 1920). The impact on subgeneric classification of the differences among the non-Californian species discussed in these papers is beyond the scope of the present review.

(Tagelus)

Without a radial strengthening rib; periostracum thin, easily worn off; white within.

Tagelus (Tagelus) affinis (C. B. Adams, 1852)

(Figures *17* and 25)

Solecurtus affinis C. B. Adams
Adams, 1852a: 524, 548 [1852b: 300, 324]
Carpenter, 1857b: 245, 280, 301
Carpenter, 1857c: 27
Carpenter, 1864a: 369 [1872: 205]
Carpenter, 1864c: 553 [1872: 39]

[*Tagelus*]
Dall, 1898: 59, 61
I. Oldroyd, 1925: 187
Burch, 1945a: 23, 29 (text fig.); 1945b: 18
Hertlein & Strong, 1950: 222, 251; plt. 1, figs. 9, 11
Turner, 1956: 29; plt. 29, figs. 17, 18
Keen, 1958: 192 - 193; fig. 470
Olsson, 1961: 351, 535; plt. 62, figs. 4, 4a
Keen, 1971: 245 - 246; fig. 615

Type Material:
MCZ 186363, lectotype (Turner, 1956), pair, 57 mm; MCZ 186559, paralectotypes, 2 pairs. Figure *17*.

Type Locality:
West coast of Panama; C. B. Adams.

Nomenclatural Commentary:
The relationship of this species to *Tagelus (T.) affinis irregularis* Olsson, 1961, described from Ecuador, remains uncertain. It may be a distinct species or a synonym. I agree with Keen (1971) that *T. (T.) longisinuatus* Pilsbry & Lowe, 1932, named as a subspecies of *T. (T.) affinis,* is distinct.

Description:
Medium-sized for genus (to 60 mm); relatively short; inflated; relatively heavy; nearly equilateral; ends broadly rounded; postero-dorsal slope not sharply angled or expanded; smooth, with growth striae only; periostracum straw-colored to dark, often present only on outermost margin; white within. Pallial sinus extends past beaks in Californian specimens. Other internal details shown in Figure 25.

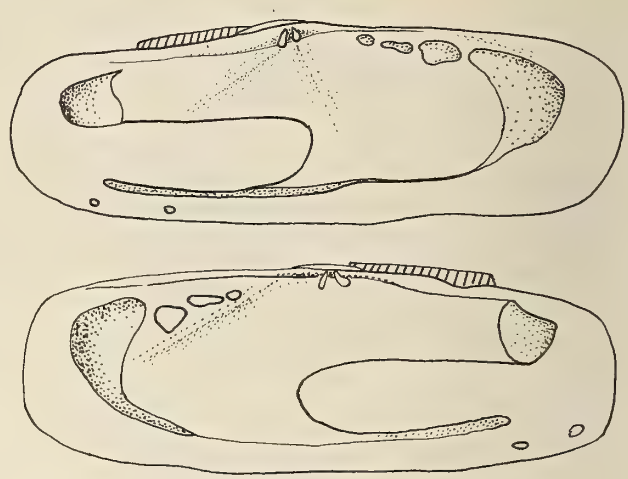

Figure 25

Tagelus (Tagelus) affinis

Internal view of valves
MCZ 257632, Cayucos, California; 67 mm

Geographic Distribution and Ecology:
Cayucos, California (MCZ 175497), to Sua and Manglaralto, Ecuador (Olsson, 1961), with many intermediate records. This species is found intertidally in protected bays in mud (Burch, 1945a). In the Panamic province it has been reported at a depth of 73 m (Hertlein & Strong, 1950).

Material seen:
44 lots from area of study.

Geologic Distribution and Biogeography:
Tagelus (T.) affinis is known as a fossil only from the west coast of Mexico in the Pleistocene of Bahía de Santa Inez, Baja California Sur (Hertlein, 1957), Isla Tibu-

Explanation of Figures *16* to *19*

Figure *16*: *Nuttallia nuttallii.* Holotype of *Sanguinolaria orcutti,* USNM 333118; 130 mm
Figure *17*: *Tagelus (Tagelus) affinis.* Lectotype of *Solecurtus affinis,* MCZ 186363; 57 mm

Figure *18*: *Tagelus (Tagelus) californianus.* Lectotype (herein) of *Solecurtus (Cultellus) californianus,* BM(NH) General collection 1861.5.20.136; about 102 mm

Figure *19*: *Tagelus (Mesopleura) subteres.* Holotype of *Solecurtus (Cultellus) subteres,* BM(NH) Nuttall collection 1861.5.20.125; 45 mm

Figure *16*

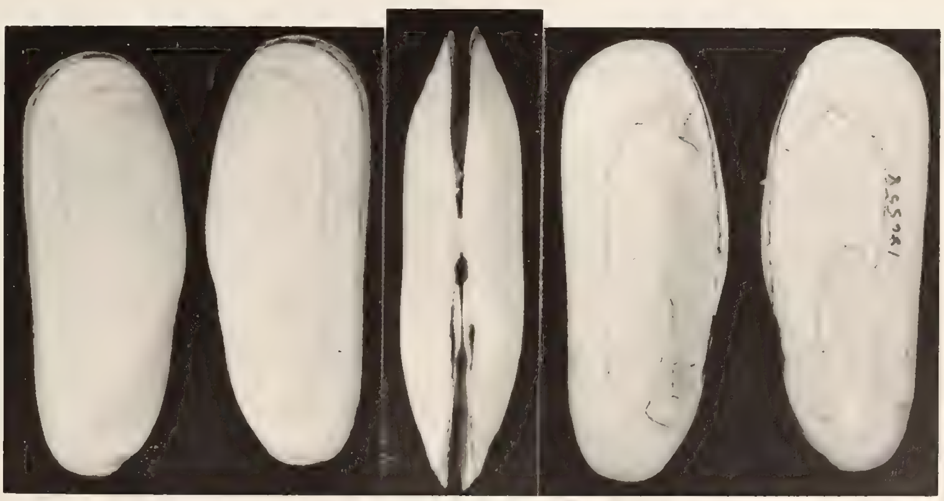

Figure *17*

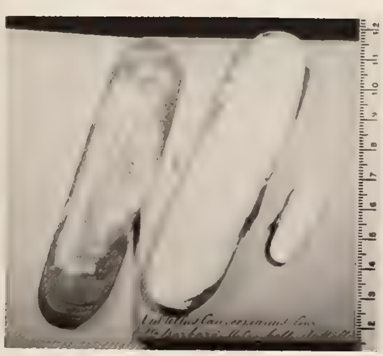

Figure *18*

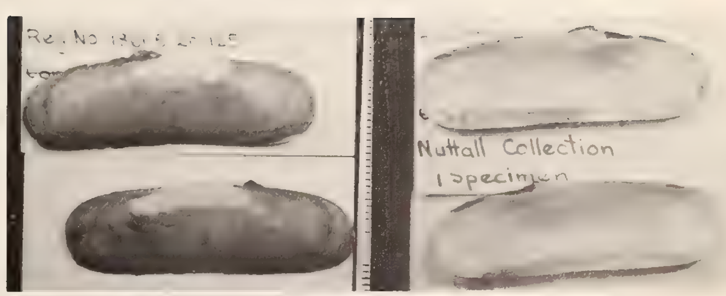

Figure *19*

ron, Sonora (DURHAM, 1950), and Islas Tres Marías, Nayarit (HERTLEIN & EMERSON, 1959).

It is very close to *Tagelus (T.) plebeius* ([Lightfoot], 1786), a common Caribbean species, from which it differs in being less expanded postero-dorsally.

Tagelus (Tagelus) californianus (Conrad, 1837)

(Figures *18* and 26)

Solecurtus (Cultellus) californianus Conrad [*californicus, californiensis,* of authors, misspellings]

CONRAD, 1837: 333; plt. 18, fig. 3
CARPENTER, 1857a: 212
CARPENTER, 1857b: 195, 231, 284, 301, 349, 351
CARPENTER, 1864c: 526, 536, 540, 592, 638, 684 [1872: 12, 22, 26, 78, 124, 170]
SOWERBY, 1874: plt. 8. fig. 36

[*Tagelus*]

DALL, 1898: 59, 60, 61
DALL, 1900: 984
ARNOLD, 1903: 169
I. OLDROYD, 1925: 186 - 187
GRANT & GALE, 1931: 384, 924; plt. 21, figs. 2a, 2b, 3
BURCH, 1945a: 23, 29 - 30 (text figs.); 1945b: 18

[*Tagelus (Tagelus)*]

HERTLEIN & STRONG, 1950: 222 - 223, 251; plt. 1, fig. 1
KEEN, 1958: 192; fig. 471
KEEN, 1966a: 171
KEEN, 1971: 245 - 246; fig. 616
HERTLEIN & GRANT, 1972: 306 - 307

Type Material:

BM(NH) General collection 1861.5.20.136, **lectotype** herein, pair, the larger of two specimens, about 102 mm; ?**paralectotype**, a smaller left valve, but probably something else mixed in from another lot; BM(NH) Nuttall collection 1854.3. 14.55, **paralectotype**, right valve; USNM 11820, **paralectotype**, pair. Figure *18*.

Type Locality:

"Neighbourhood of" Santa Barbara, California; T. Nuttall, in salt marshes.

Nomenclatural Commentary:

See "Geologic Distribution and Biogeography."

Description:

Large for genus (to 110 mm); shell longer than in the other northwest American species; relatively flattened; valves moderate in thickness; nearly equilateral; anterior end rounded; posterior end slightly truncate; postero-dorsal slope more or less set off, sometimes forming a noticeable "wing"; sculpture of growth lines only; periostracum straw-colored to dark, rough, present only ventrally and on ends of shell in adult; white within. Pallial sinus extending past beaks. Other internal details shown in Figure 26.

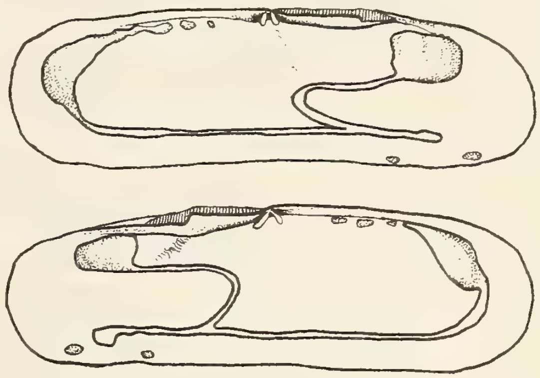

Figure 26

Tagelus (Tagelus) californianus

Internal view of valves
MCZ 21793, Santa Barbara, California; 87 mm

Geographic Distribution and Ecology:

Humboldt Bay, California (FITCH, 1953 and *in litt.*), along the Pacific coasts of California and Baja California, throughout the Gulf of California, to "northern" Mexico (KEEN, 1971), with many intermediate stations represented in collections. It is found intertidally in the muddy sand of protected bays, living in permanent burrows up to 40 cm deep. It approaches the surface to filter-feed (WEYMOUTH, 1921; BURCH, 1945a; YONGE, 1952; FITCH, 1953; POHLO, 1966). Ciliary currents were studied by KELLOGG (1915).

Material seen:

182 lots from area of study.

Geologic Distribution and Biogeography:

This species is known in the late Pleistocene from Tomales Bay, California (DICKERSON, 1922; WEAVER, 1949; JOHNSON, 1962), to Bahía Magdalena, Baja California Sur (JORDAN, 1924, 1936), with many intermediate records. It has also been recorded in the Pleistocene of Isla Monserrate (EMERSON & HERTLEIN, 1964) and Bahía de Santa Inez (DURHAM, 1950; HERTLEIN, 1957), Baja California Sur, and of Puerto Peñasco, Sonora

(Hertlein & Emerson, 1956). It has been reported from the early Pleistocene of southern California in the northwestern portion of the Los Angeles Basin (Rodda, 1957), the San Pedro area (Arnold, 1903; Valentine & Meade, 1961), and, in error (according to Hertlein & Grant, 1972), from the Salton Sea area (Orcutt, 1889). There are records from southern California formations transitional between the Pliocene and the Pleistocene and from the Pliocene of California and Baja California. I am aware of no Miocene records and there are no similar Asian species.

On the other hand, this species is closely allied to other species of the Panamic province. *Tagelus (T.) violascens* (Carpenter, 1857c) was described from southwestern Mexico and is similar and possibly identical with *T. (T.) dombeii* (Lamarck, 1818), type species of the generic unit *Solecurtellus* Ghosh, 1920, from South America. Records of *T. (T.) californianus* from Panama may really be of *T. (T.) dombeii,* which differs from *T. (T.) californianus* in being smaller, more inflated, tending to be narrowed just posterior to the beaks, to be tinged with purple externally, and to have a more shiny periostracum. The unique type specimen of *T. (T.) violascens* seems to be more similar to *T. (T.) dombeii* in some of these features, but a careful study of material from the entire Panamic province must be undertaken before we can properly understand the relationships among these taxa.

(Mesopleura) Conrad, 1868

[Type species: *Solen bidentatus* Spengler, 1794, by SD of Stoliczka, 1871 = *Solen divisus* Spengler, 1794]

With a radial strengthening rib and an adherent, often shiny periostracum; dark purple, particularly within.

Tagelus (Mesopleura) subteres (Conrad, 1837)

(Figures *19* and 27)

Solecurtus (Cultellus) subteres Conrad
Conrad, 1837: 333; plt. 17, fig. 10
Carpenter, 1857a: 212
Carpenter, 1857b: 195, 231, 234, 301, 349, 351
Carpenter, 1864c: 536, 575, 638 [1872: 22, 61, 124]
Sowerby, 1874: plt. 8, fig. 39

[*Tagelus*]
Dall, 1898: 60 - 61

[*Tagelus (Mesopleura)*]
Dall, 1900: 985
I. Oldroyd, 1925: 187
Grant & Gale, 1931: 385
Burch, 1945a: 23, 29, 31 (text fig.); 1945b: 18
Hertlein & Strong, 1950: 225, 251; plt. 1, figs. 12, 13
Keen, 1958: 194; fig. 476
Keen, 1966a: 171

Type Material:
BM(NH) Nuttall collection 1861.5.20.125, holotype, pair, 45 mm. Figure *19.*

Type Locality:
"Vicinity of" Santa Barbara, California; T. Nuttall.

Nomenclatural Commentary:

Specimens of this species (as well as a few of *Tagelus californianus*) account for Californian records of the Panamic species *T. (M.) politus* (Carpenter, 1857c) [1], which was described from Mazatlán, Sinaloa, Mexico. It is distinct and occurs from Cabo San Lucas, throughout the Gulf of California, and south to Tumbez, Peru (Olsson, 1961; Keen, 1971). This tropical species is smaller, longer posteriorly, more inflated, more strongly angled postero-dorsally, darker purple in color, and has a darker, thinner periostracum. It occurs offshore, while *T. subteres* is characteristic of bays.

Description:

Medium-sized for genus (to 55 mm); relatively short; moderately inflated; moderate in thickness; equilateral to slightly longer posteriorly; ends rounded; periostracum

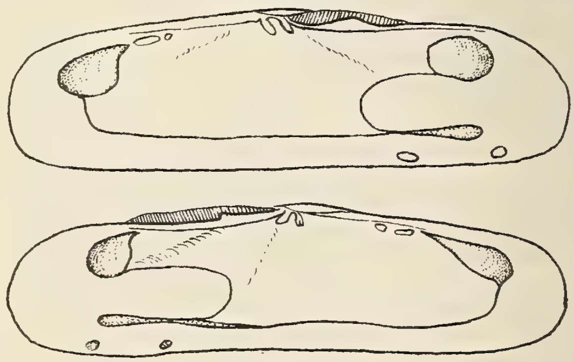

Figure 27

Tagelus (Mesopleura) subteres

Internal view of valves
MCZ 54944, Anaheim Bay, California; 49 mm

[1] Could this species be preoccupied by *Solen politus* Wood, 1828 [3; plt. 1, *Solen* figure 6]? Hanley (1842) suggests that it may be a *Tagelus (Mesopleura).*

dark, shiny; externally with a faint radial purple ray; internally purple and shiny. Other internal details shown in Figure 27.

Geographic Distribution and Ecology:

Morro Bay, California (SBMNH 13567), to Laguna San Ignacio, Baja California Sur (UCB 2783), with several intermediate records. Records from farther south are probably of *Tagelus (Mesopleura) politus,* as is the case with the specimen reported from Cabo San Lucas by HERTLEIN & STRONG (1950). This species occurs in the intertidal area of bays in sand (BURCH, 1945a).

Material seen:

108 lots.

Geologic Distribution and Biogeography:

Tagelus (Mesopleura) subteres has been recorded in the late Pleistocene from Santa Monica, California (VALENTINE, 1956), to Bahía San Quintín, Baja California Norte (JORDAN, 1926). There is also a record in the Pleistocene of Isla Monserrate, Baja California Sur, in the Gulf of California (EMERSON & HERTLEIN, 1964), which is considered doubtful and should be carefully reexamined.

Its biogeographic affinities are to *Tagelus (Mesopleura) politus,* to other species of this subgenus in the Panamic province, and to *T. (M.) divisus* (Spengler, 1794) of the Caribbean.

ECOLOGY

The ecological information available about species of the Psammobiidae is summarized in the following table:

Most species of the Psammobiidae are characteristic of a protected environment, either of bays or offshore. Only one species, *Gari californica,* occurs in rubble in fairly exposed areas.

The abundance of species is reflected in their frequency in collections:

Table 2

Species	Number of lots seen
Tagelus californianus	182 [1]
Gari californica	164
Nuttallia nuttallii	121
Tagelus subteres	108
Heterodonax pacificus	93 [1]
Tagelus affinis	44 [1]
Gari edentula	31
Gari regularis	2

[1] not including specimens from Panamic province south of area studied

BIOGEOGRAPHY

In my previous papers on the Tellinidae and the Semelidae (COAN, 1971, 1973), I defined the molluscan provinces mentioned here as follows:

Aleutian – Eastern Aleutian Islands to Cape Flattery, Washington

Table 1

Species	Depth range meters	Bottom type	Coastal exposure
Gari californica	0 - 168	rubble to sand	protected to exposed, bays and offshore
Gari edentula	5 - 137	fine sand	protected, offshore
Gari regularis	18 - 37	sand	protected, offshore
Heterodonax pacificus	intertidal only	sand	protected, bays
Nuttallia nuttallii	0 - 10	sand	protected, bays and rarely offshore
Tagelus affinis	intertidal only	mud	protected, bays
Tagelus californianus	intertidal only	muddy sand	protected, bays
Tageles subteres	intertidal only	sand	protected, bays

Oregonian – Cape Flattery, Washington, to Point Conception, California

Californian – Point Conception, California, to Punta Eugenio, Baja California Sur

Panamic – Punta Eugenio, Baja California Sur, to Punta Aguja, northern Peru

The following table demonstrates the predominance of members of the Psammobiidae in warmer waters, in contrast to the Tellinidae, and similarly to the Semelidae.

Table 3

Aleutian	Oregonian	Californian	Panamic
4. *Gari californica*			
	3. *Nuttallia nuttallii*		
	3. *Tagelus affinis*		
	3. *Tagelus californianus*		
	3. *Tagelus subteres*		
		2. *Gari regularis*	
		2. *Heterodonax pacificus*	
		2. *Gari edentula* ?	

In this table, the following abbreviations are used:

2. species occurring in 2 provinces
3. species occurring in 3 provinces
4. species occurring in 4 provinces

Distributions in the Pleistocene are less similar to distributions in the Recent fauna than is the case of members of the Tellinidae or the Semelidae. Recent distributions are wider than those in the Pleistocene. For example, *Gari californica,* in spite of its basic alliance with a similar Asian species, now occurs in Alaska, whereas in the Pleistocene it may only have occurred as far north as San Nicholas Island in southern California. Similarly, *Nuttallia nuttallii* now occurs as far north as Bodega Bay, whereas in the late Pleistocene it is known only as far north as Summerland in southern California. *Tagelus affinis* may occur as far north as Cayucos, whereas in the late Pleistocene it is reported only from the Panamic province; *T. californianus* now occurs in Humboldt Bay, but only as far north as Tomales Bay in the late Pleistocene; *T. subteres* is now found in Morro Bay, but in the late Pleistocene it has been reported only as far north as Santa Monica.

Nuttallia nuttallii has apparently had the longest history of any member of this family on the northwest American coast, with closely similar species reported from the Miocene and the genus present from the Eocene. There are also related species, including a homologue living in Japan. *Gari californica,* dating from the Pliocene, is homologous to a Japanese species. *Gari edentula* also occurs as far back as the Pliocene, but there are no known related species in the Atlantic or in the western Pacific.

All three species of *Tagelus* and the one *Heterodonax* show closest relationships to species in the Panamic province. *Tagelus affinis* and *Heterodonax,* both recent arrivals in northwestern America, additionally have homologues in the Caribbean.

Literature Cited

[All works cited in the text, including sources of taxonomic units, are listed. Volume, bulletin, monograph, memoir, professional paper, and special paper numbers are in bold face; series numbers, in parentheses, precede volume numbers; issue numbers, in parentheses, follow volume numbers; supplementary information, such as secondary methods of listing volumes, part numbers, and parenthetical statements, are given in brackets. Plates, portraits, text figures, maps, and charts are listed, but not tables. Exact publication dates are given when possible.]

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A New Species of *Conus* from Indonesian Waters

BY

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(2 Plates)

THROUGH THE KIND OFFICES of Mr. Victor Wee, of Singapore, a series of specimens of a remarkable cone was submitted to me for study. I take pleasure in describing this new cone in honor of Mr. Wee.

Conus (*Textilia*) ***vicweei*** Old, spec. nov.

(Figures *1–3*; *5*)

Description: Shell cylindrical, with a low spire; surface smooth, practically devoid of sculpture; spire of holotype quite flattened, (Figures *5*a & *5*b). Protoconch produced, smooth, mamillate; opaque white in color and consisting of 2½ whorls. Post-nuclear whorls nine in number, the earliest two beaded. Suture distinct, with five to six threads on spiral whorls; threads with very fine beads, imparting a slightly cancellate appearance to spire. Spire with alternating pattern of white and tan. Base with about a dozen raised spiral ribs.

Body whorl smooth, polished, with faint growth lines. Coloration rich chestnut with two revolving bands of ivory white. Bands in the form of tightly-packed chevrons. White markings irregularly distributed over surface between bands. Coloration pales out adjacent to the lip, and on apertural side, where it is reduced to a delicate purplish-brown. A smaller, third white band is discernible above the base on the apertural side. Aperture white throughout.

Height of holotype: 66 mm.

In the holotype (Figures *1*a & *1*b), the upper line of white markings is solid, while the lower one is divided throughout its length. Paratypes "A" and "B" have the upper bands finely divided, while the lower one is tricincted (three-banded).

In Paratype "A" (Figures *2*a & *2*b), the spire is produced at an angle of about 110°. The nucleus is broken in this specimen. Paratype "B" (Figures *3*a & *3*b), has a lower spire, with an angle of approximately 130°. The mamillate nucleus is missing in this specimen.

Operculum and soft parts are unknown.

Holotype: Depository, American Museum of Natural History, no. 173710. Trawled in 55–60 fms., Northwest of Sumatra, Indonesia. On sand and sponge bottom, in mid-August, 1972.

Type Locality: 50–60 fms. off Northwest Coast of Sumatra, Indonesia.

Paratype "A": Collection of Victor Wee, Singapore. Collected with the holotype, in the same haul. Shell 73.3 mm + in length.

Explanation of Figures *1* to *3*

Conus (*Textilia*) ***vicweei*** Old, spec. nov.

Figure *1:* Holotype (AMNH no. 173710); trawled 50–60 fathoms, off Northwest coast of Sumatra, Indonesia. × 1.3
Figure *2:* Paratype "A" (Victor Wee collection); trawled 50–60 fathoms, off Northwest coast of Sumatra, Indonesia. × 1.3
Figure *3:* Paratype "B" (Victor Wee collection); trawled 45 fathoms Northwest of Sumatra. × 1.3

Photographs courtesy of American Museum of Natural History

Figure *1* a

Figure *1* b

Figure *2* a

Figure *2* b

Figure *3* a

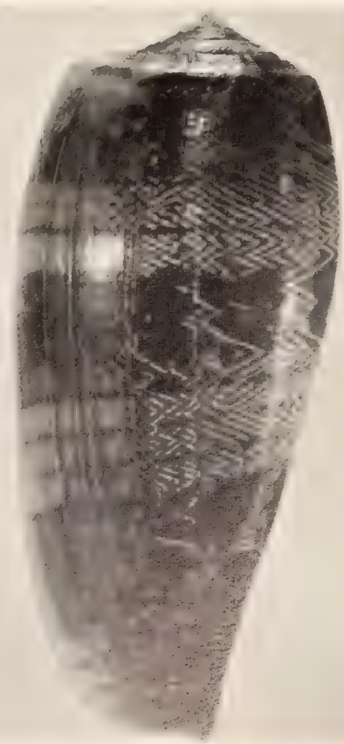

Figure *3* b

Paratype "B": Collection of Victor Wee, Singapore. 45 fms. trawled northwest of Sumatra. Shell 73 mm + in length.

Diagnosis: The new species appears closest to *Conus (Textilia) cervus* Lamarck, 1822. From that species it may be readily distinguished by its smaller size, and radically different color pattern.

Discussion: *Conus vicweei* is referable to the subgenus *Textilia* Swainson, 1840, a small group of Indo-Pacific cones with smooth, inflated shells and with flared lips. Species assigned here are *Conus bullatus* Linnaeus, 1758 (type species: SD Cotton, 1945), *Conus adamsoni* Broderip, 1836 (=*C. rhododendron* Jay, 1839), *C. cervus* Lamarck, *C. julii* Liénard, 1870, *C. stercusmuscarum* Linnaeus, 1758, and probably *C. dusaveli* H. Adams, 1872. These cones are of subtidal habitat, and are of uncommon to rare occurrence. From studies conducted on the feeding habits of *Conus* by various workers, Lim, 1969, in particular, it would appear that all species of *Conus* assigned to this group are piscivores.

Although described by Lamarck in 1822, *Conus cervus* remains one of the rarest of shells. Lamarck gave a brief Latin description, citing no locality. His type is in the Lamarck collection in the Muséum de Genève (*fide* Mermod, 1947). The species was well illustrated in the 19th Century monographs: G. B. Sowerby 2nd (1833 *Conus* fig. 24, as *C. bullatus* Lam. var.); Reeve (1843, plt. 22, fig. 124); Kiener (1846, plt. 74, fig. 1, plt. 75, fig. 1); Sowerby 2nd (1858, plt. 208, fig. 548); Chenu (1859, p. 250, fig. 1539); Weinkauff (1875, plt. 59, fig. 6); Kobelt (1878, plt. 34, fig. 1); and Tryon (1884, plt. 28, ref. to fig. 78 only). The only localities cited were "Amboyna" (Sowerby 2nd, 1858) and "Molukken" (Kobelt; Weinkauff) and "Moluccas" (Tryon).

Reeve described *Conus cervus* as "rather large, cylindrically ovate, a little inflated; pale rosaceus yellow, encircled with unequal fillets of promiscuously articulated white and dull brownish-yellow; spire short, spirally striated, apex pale rose-colour; interior of the shell white." Reeve's figured specimen, from the collection of Stainforth is now in the National Museum of Wales (*fide* Dance, 1969); this specimen is also figured by Dance, 1969; 1972.

An old specimen in the American Museum of Natural History, #11463, was received from the William A. Haines collection in 1888. The American Museum specimen measures 89 mm in length, and is 45.5 mm wide. About ten whorls are discernible on the spire, the early portion being eroded due to "doctoring" many years ago. Locality is given as "Amboyna." This may be the only specimen preserved in a museum in the United States. A specimen was reported to be in the private collection of Mrs. S. L. Williams of Chicago around the turn of the century by Webb (1948: 206) and Dance (1966, p. 219); Webb also (1948, plt. 10, fig. 3) figures one from the A. L. Ward collection.

Three specimens are preserved in the collections of the British Museum (Natural History). Two are labeled as having come from "Amboyna," *ex* Mrs. de Burgh's collection, the third 111 mm × 54 mm, lacks data.

An especially well-preserved specimen (Figures *4*a & *4*b) in Zoölogisch Museum, Amsterdam, measures 103.6 mm, and is labeled "Moluccas, Indonesia." This may be the same specimen figured by Valentyn (1754; plt. 10, fig. 91). Both the New York and Amsterdam specimens are heavily infested by boring sponges.

Dance (1972) stated that to his knowledge, "all the known specimens were collected before 1900." Mr. Victor Wee (*in litteris*) has informed me, however, "I collected two very fine, perfect specimens of *Conus cervus* about 3 years ago in the Bangka Straits, Indonesia. They had a darker background than the one in *Rare Shells* by P. Dance, and the transversal dots and dashes were reddish-orange in colour."

The exact status of *Conus cervus* caused some confusion in the 19th Century: Sowerby 2nd figured it as "*Conus bullatus* Var.," and used the name *Conus cervus*, for a Red Sea species, *C. (Gastridium) cuvieri* Crosse, 1858. Tryon (1884) treated *C. cervus* Lamarck as a species, with *C. cuvieri* as a "Var."

Reeve stated . . . "*Conus cervus* is so clearly allied to . . *Conus bullatus* . . that . . . it may prove to be a gigantic variety of that species. The difficulty of uniting the *Coni* [sic] *cervus* and *bullatus* under one species, with a proper degree of certainty arises from our having no intermediate examples."

Reeve's observation, published over 130 years ago, could equally well apply to *Conus vicweei* today. It would seem strange for two such distinctly patterned "races" of *C. cervus* to occur in such relatively close geographical proximity. *Conus vicweei* has been trawled off the west coast of Sumatra, but it may be found to range northward into the Mergui Archipelago. *Conus cervus* has been reported off the east coast of Sumatra in the Bangka Straits, and from the classical localities of "Amboina" and Moluccas." None of the specimens or figures of *Conus cervus* examined bears a hint of the distinctive pattern of *C. vicweei*. The available data indicate that it is a distinct species.

ACKNOWLEDGMENTS

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Explanation of Figures *4, 5*

Figure *4: Conus (Textilia) cervus* Lamarck, 1822, Moluccas, Indonesia (collection Zoölogisch Museum, Amsterdam). × 9/10

Photographs courtesy of Zoölogisch Museum, Amsterdam

Figure *5:* Holotype of *Conus (Textilia)* ***vicweei*** Old, spec. nov.
a: Detail of spire. × 6
b: View of spire and nucleus. × 9

Enlargements courtesy of American Museum of Natural History

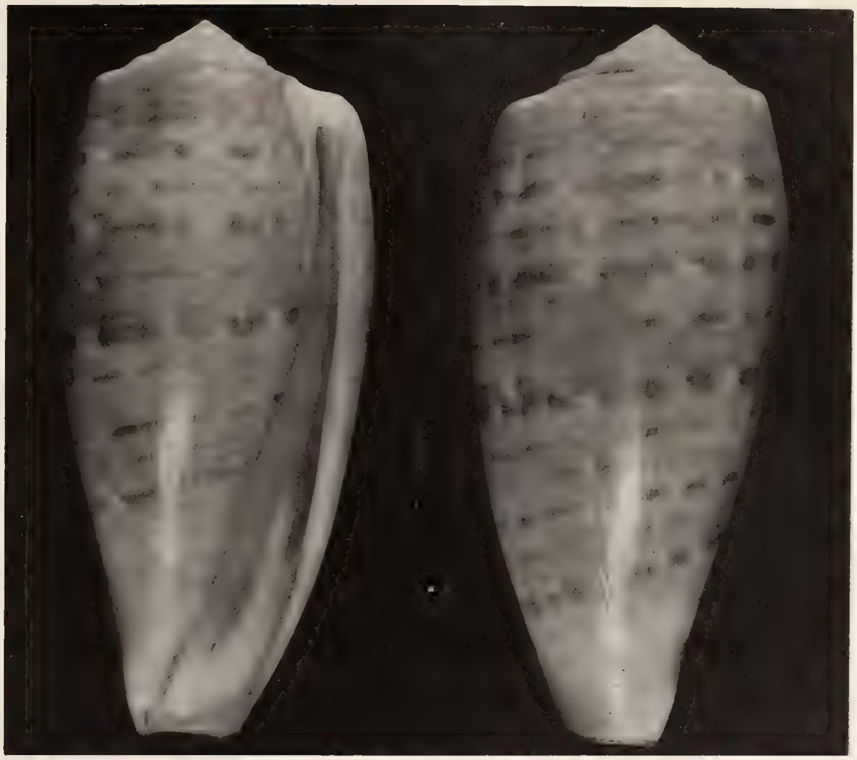

Figure 4a Figure 4b

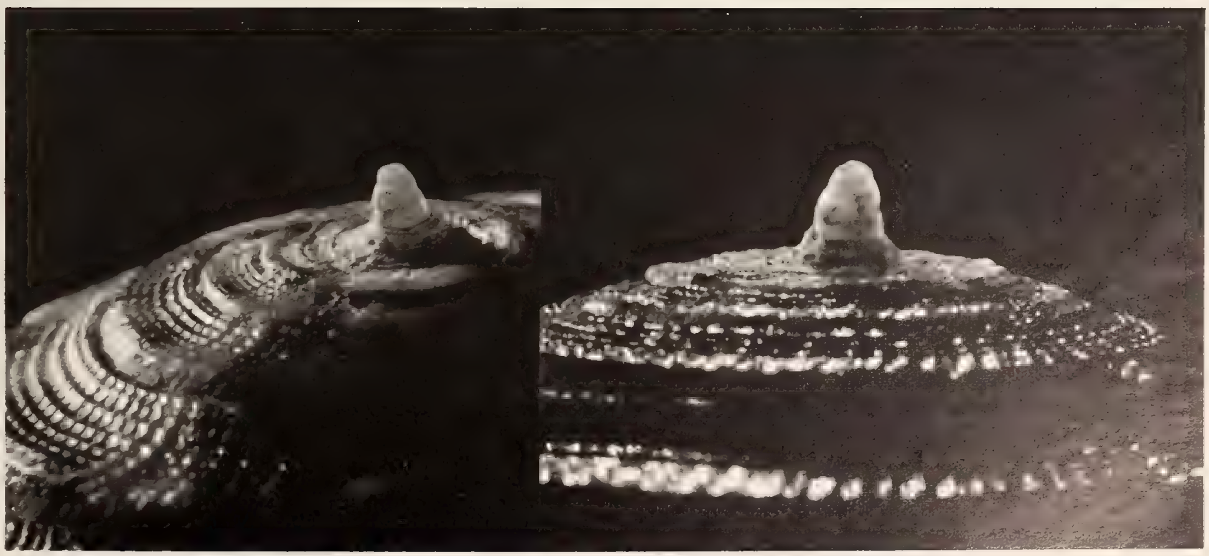

Figure 5a Figure 5b

Reproduction, Development, and Feeding of the Australian Marine Pulmonate, *Trimusculus (Gadinia) conica*

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(1 Plate; 2 Text figures)

Trimusculus (Gadinia) conica (Angas, 1867) is a marine pulmonate limpet found along the rocky outer coast of Australia from Queensland to the south coast of Western Australia (Cotton, 1959) (Figure 1). The present observations on feeding and reproduction were made on populations along the coast of New South Wales from December 1966 until September 1967.

The family Trimusculidae has a worldwide distribution, with representatives recorded from the Mediterranean, Africa, the west coast of North and South America, as well as in Australia, Japan and many Pacific Islands (Hubendick, 1946).

Previous observations on live *Trimusculus* have been made on the European species *T. garnotii* (Payraudeau, 1839) by Lacaze-Duthiers (1885a, 1885b), while Dall (1870) and Yonge (1958, 1960) worked on *T. reticulatus* (Sowerby, 1835) in California. The most extensive work on the genus is that of Schuman (1911), and is largely concerned with anatomy and histology. Dieuzeide (1935) and Hubendick (1945) gave particular attention to the relationship between the Trimusculidae and Siphonariidae, as evidenced in their anatomy.

MATERIALS AND METHODS

Colonies were sampled for eggs every two weeks from February 14, 1967 until September 24, 1967. Collections were made at either Cape Solander, Boat Harbour, or Oak Park, Cronulla (Figure 1). The first two sites are located on the Kurnell Peninsula (34° S, 151°10′E) just south of Botany Bay; Cronulla lies 3 miles south of Boat Harbour.

Adults were kept in aquaria in running seawater. Unhatched larvae (still in the egg cases) were relaxed for 25 minutes in a 1 : 1 solution of $2\frac{1}{2}\%$ magnesium chloride and seawater, with a few drops of nickel sulfate solution added, plus a few menthol crystals.

RESULTS

Trimusculus conica occurs in the low intertidal zone of exposed rocky coast in New South Wales. The animals are clustered on the underside of the roofs of rocky overhangs and caves. Distribution along an area of coast is often spotty; for example, only 2 populations were found in one boulder field approximately 400 feet (120m) long. However, within the area where *T. conica* is found, individuals are usually numerous and tightly packed together.

The shell of *Trimusculus conica* is that of a typical limpet (Figure 2) and adults are commonly 2 to $2\frac{1}{2}$cm in diameter. Young specimens have a creamy white shell, with fine ribs radiating out from the apex. *Trimusculus conica* has a broad flat foot (Figure 3) and can attach itself securely to rocks in areas of heavy wave shock. The foot is bordered by a deep pallial groove. Two large folded flaps of tissue, the oral lappets, surround the mouth. There are no tentacles, and the eyes lie on the dorsal side of the head just behind the lappets.

Adults are often fastened to the substratum by a thin flexible sheet of brown translucent material which adheres partly to the foot and partly to the rock when the animal is pried loose. PAS stains (Coleman-Feulgen, counterstained with 0.2% light green) indicated the presence of carbohydrates and a mucopolysaccharide. Specimens kept for 3 months in the laboratory secreted new "glue" beneath the foot, but those kept for only a week or two did not do so.

The normal, undistorted adult shell is fairly regular in outline (Figure 2) but most individuals living in crowded groups have irregularly shaped shells. Shell growth, such as seen in Figure 4, has been inhibited by juxtaposition of neighboring specimens of *Trimusculus conica.* In colonies where specimens were removed over an 8-month period of sampling, new shell growth occurred on the margins of *T. conica* that had lost their nearest neighbors.

Figure 1

Collecting sites in New South Wales, indicated by black dots. Inset shows range of *Trimusculus conica* in Australia

Explanation of Figures *2* to *9*

Figure *2*: Normal shell growth of *Trimusculus conica*
Figure *3*: Preserved specimen of *Trimusculus conica*, ventral view F = foot; O = oral lappets; P = pallial groove
Figure *4*: Shell of *Trimusculus conica* where crowding has inhibited growth along two edges
Figure *5*: Shell of single specimen of *Trimusculus conica* almost completely covered with barnacles
Figure *6*: Egg collar of *Trimusculus conica*. Lower edge attaches to substratum and collar projects into pallial groove of adult. Two collars are brooded by each individual
Figure *7*: *Trimusculus conica* emerging from egg case
Figure *8*: Newly hatched specimen of *Trimusculus conica* crawling on egg casing. Larval foot is extended in front of shell; eyes and oral lappets lie beneath transparent front portion of shell
Figure *9*: Shell of young *Trimusculus conica*. Larval shell remains attached at apex

Figure 2 1 mm

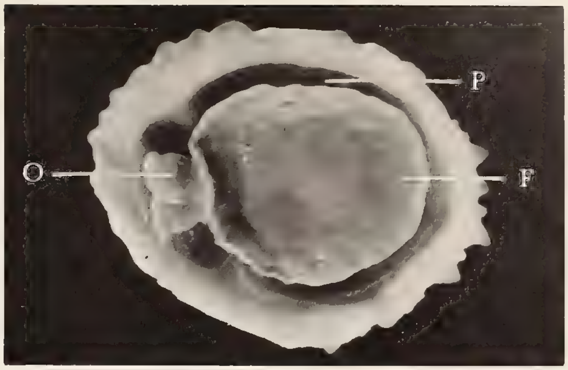

Figure 3 2 mm

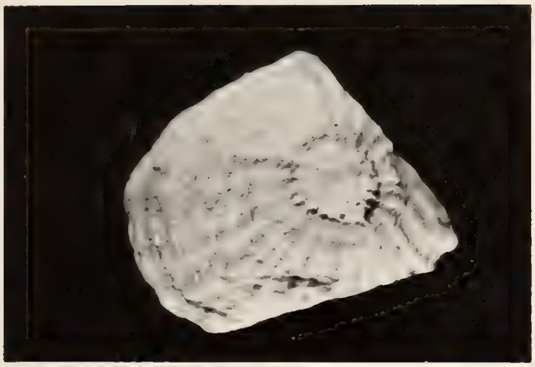

Figure 4 5 mm

Figure 5 5 mm

Figure 6 2 mm

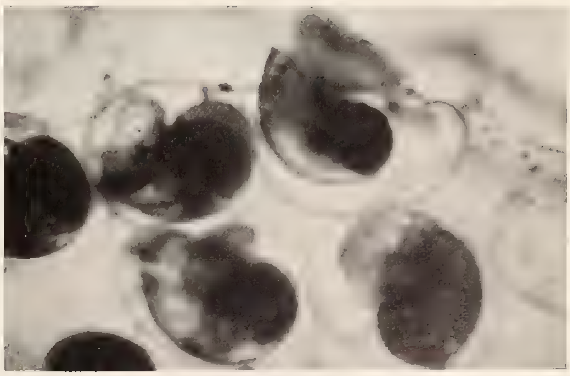

Figure 7 0.1 mm

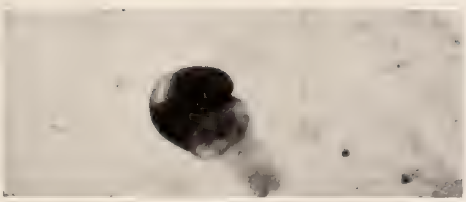

Figure 8 0.1 mm

Figure 9 1 mm

Specimens were often covered with barnacles (Figure 5), coralline and non-calcareous algae, and serpulid worms. One individual had a serpulid worm tube (*Galeolaria caespitosa*) attached to both its shell and to the rock on which it lived.

There was no indication that movement did or could occur in a colony even when it was submerged: individuals were found tightly packed together in groups and fastened to the substratum. In addition, large adults did not move about when kept in the laboratory.

FEEDING

Since it was clear that the adults do not move around in their habitat, it became of interest to study their method of feeding. It seemed possible that the large oral lappets were involved in the capture of plankton. Adults kept in a strong flow of water in the laboratory would raise the anterior margin of their shells, extending the oral lappets as much as 5mm beyond the shell margin. The engorged lappets were held in a scoop-like position slightly above the substratum. However, no evidence of associated feeding behavior was obtained in the laboratory.

Trimusculus conica possesses a radula and can obtain food by grazing. The stomach of specimens collected in the field contained diatoms and amorphous debris, which bore a resemblance to scrapings which were taken from shells of nearby *T. conica*. Algal sporlings were common in the gut and were similar in size and appearance to those of *Ulva lactuca* which occurs in the area.

One adult lived for several months on the bottom of a container on the seawater table in the laboratory. A thin layer of brownish diatoms accumulated everywhere except in an area approximately 2mm wide around the limpet's head. Apparently sufficient nutrition was derived from grazing in this area since this animal remained healthy throughout its stay in the laboratory.

In addition, stomach contents of specimens brooding eggs were examined. The egg strands are attached to the rock (see next section) and prevent the adult from moving away. Adults that were brooding fully developed eggs had sand grains, particles of algae, sporlings, and debris in their stomach. This was further proof that feeding takes place while the animals are stationary, since the presence of well developed larvae indicated that the eggs had been brooded for several days, at least.

REPRODUCTION

Eggs are laid in two creamy white collars approximately 14mm long and 4mm wide (Figure 6). The collars lie on each side of the foot, extending upward into the pallial groove, but attached along their lower length to the rock beneath. Each collar contains approximately 900 eggs in varying stages of development. Adults that are brooding eggs can be readily identified in populations when the air temperatures are warm, because their shells are lifted slightly off the rock.

Some egg collars were always present in the population throughout the 8-month period of sampling (February through September). Quantitative sampling was not done because of the small number of colonies accessible; however, when eggs seemed more abundant, the abundance appeared to be correlated with a particular locality, rather than the season.

Development is direct, with the veliger stage (Figure 10A) being passed within the egg. Before hatching, the velum gradually becomes smaller (Figures 10B, 10C) and by the time of hatching (Figures 10D, 10E) it has been transformed into miniature oral lappets. When hatching time approaches, the young individuals inside the egg cases can be seen rubbing the case with the foot. When the case is broken (or eroded), the young *Trimusculus conica* crawls out (Figure 7) and moves about on an enormously extensible foot (Figures 8 and 10E).

Attempts were made to grow the young in the laboratory, but the young did not feed. Observations of later growth stages were made on individuals found living among the fine matting of red algae that grew on some of the adult shells. New shell is at first laid down along the anterior margin of the larval shell (Figure 10G). The operculum is lost, probably at this time. When the shell has grown all around the margins of the larval shell and the adult limpet shape is discernible, the foot and oral lappets are also similar (Figure 10H) to those found in the adult. The larval shell remains attached to the adult shell (Figure 9) until it is eroded or covered over by encrusting growth.

It is not clear at what size *Trimusculus conica* becomes immobile. When specimens were brought into the laboratory, young ones would often climb up the sides of the containers until they reached the water line. Fully grown specimens did not climb or move about, and survived quite well while constantly submerged.

DISCUSSION

Trimusculus conica occupies a somewhat unique position among the intertidal limpets insofar as its way of life is concerned. Many grazing gastropods and some limpets are highly mobile and do not home. Others, such as *Acmaea scabra* (Gould, 1846) (Jesse, 1968) and *Patella* (Fretter & Graham, 1962: 498) home to precisely the

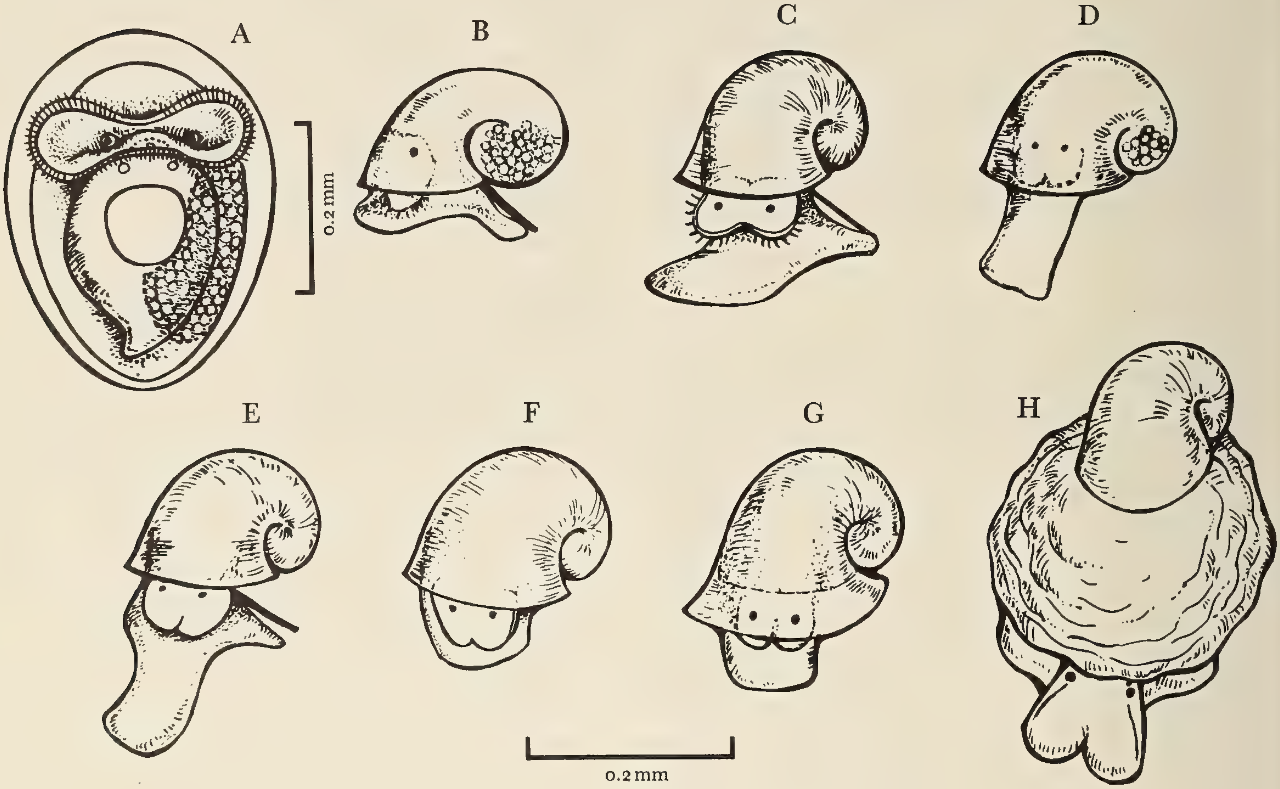

Figure 10

Early larval development of *Trimusculus conica*

A: Veliger in egg case. B, C: Pre-hatching stages, with velum being transformed into oral lappets. Foot is enlarging D, E: Newly hatched larvae, with elongate crawling foot. F: Eighteen days after hatching: foot is becoming shortened. G: First portion of adult shell has been added to larval shell. H: Oral lappets, shell and foot more closely resemble adult form. Ribbing has not yet appeared on shell

same spot as before on a rock, although they may move considerable distances to feed. The more closely related limpets of the Siphonariidae exhibit varying degrees of homing. *Siphonaria normalis* Gould, 1846 exhibits consistent homing in Hawaii (Cook, 1969), whereas only certain individuals within populations of *Benhamina obliquata* (Sowerby), a siphonariid from New Zealand, exhibit homing (Borland, 1950).

At the other extreme there is the sessile mesogastropod *Hipponix antiquatus* (Linnaeus, 1767), a grazer that is fastened in place on the rocks by a calcareous secretion, analogous to a ventral valve (Yonge, 1953). The foot is reduced to a thin membrane. *Trimusculus conica* falls in an intermediate place among these; it has what appears to be a functionally good foot, but fully grown adults are immobile and occupy permanent places on rocks in areas

of heavy surf, glued to the substrate by a thin secretion. Lacaze-Duthiers (1885b) similarly found *T. garnotii* to be immobile. Dall (1870) and Yonge (1958, 1960) describe the adults of *Trimusculus reticulatus* from California as being mobile. Both observed the animals under abnormal conditions and studies on undisturbed populations of *T. reticulatus* remain to be done.

During the period of rapid growth, *Trimusculus conica* is capable of moving about to graze for food. Once it occupies a permanent place, sufficient food is apparently obtained by grazing the region around the head. This is not unique; *Hipponix antiquatus* (Yonge, 1953) is permanently fastened in place and feeds in a similar manner.

The function of the oral lappets remains unclear. Dieuzeide (1935) doubts that they are used for feeding. It is possible they are important in respiration. Since the animal is capable of living submerged for long periods of time, an increase in the amount of body surface exposed would be a useful adaptation.

Some eggs were always present at the sites during the fall, winter and spring months. It is highly likely that reproduction in the Australian population continues throughout the year. The only other note made of egg masses is that of Lacaze-Duthiers (1885b) who found eggs during August and September in populations of the Mediterranean species *Trimusculus garnotii*. In the present study it was found that newly hatched individuals have an enormously elongate foot and that they can move about rapidly; since development is direct, this would insure dispersal from brooded eggs or crowded areas of the site.

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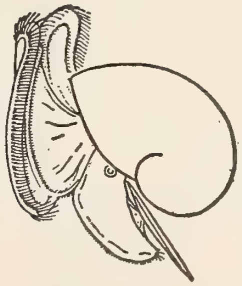

Effect of Acetazolamide on Larval Settlement of *Ostrea lutaria*

BY

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(1 Text figure)

INTRODUCTION

It has been postulated that the enzyme carbonic anhydrase (CA) is involved in the formation of molluscan shell (Stolkowski, 1951; Freeman & Wilbur, 1948; Wilbur & Jodrey, 1955) as follows:

$$CO_2+H_2O \overset{CA}{\rightleftharpoons} H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons H^+ + CO_3^{=} \rightleftharpoons CaCO_3$$

$$HCO_3^- \underset{CA}{\rightleftharpoons} CO_2+OH^- \qquad CO_3^{=} + Ca^{++} \rightleftharpoons CaCO_3$$

The strongest evidence for this is that two CA inhibitors, acetazolamide and 2-benzothiazolesulfonamide, markedly reduce the rate of deposition of calcium in the shell of *Crassostrea virginica* (Gmelin, 1791). Acetazolamide at 4.5×10^{-4} M concentration gave about 50% inhibition of calcium deposition (Wilbur & Jodrey, *op. cit.*).

In the setting process oyster larvae cement themselves permanently to a suitable substrate. These CA inhibitors were suspected of inhibiting this process and thus reducing or preventing setting. It was therefore decided to determine the effect of acetazolamide (2-benzothiazolesulfonamide not being readily available) on the setting of pediveligers of *Ostrea lutaria* (Hutton, 1873). The preliminary results reported here are surprising in that not only were the expected effects not observed but there was a significant increase in setting in the presence of acetazolamide.

METHODS AND MATERIALS

The experiment was done at sea in Foveaux Strait, the principal site of the fishery for *Ostrea lutaria* in New Zealand, to minimize the time between collection of the larvae and the start of the experiment. Numerous oysters were dredged and opened. Two oysters which were incubating late-stage pediveligers were selected for the experiment. The two groups of pediveligers were kept separate and will be referred to as Group A and Group B. Each group was suspended in 500 ml of sea water, and from each group a series of seven 50 ml aliquots was prepared. The aliquots were placed in 400 ml beakers and diluted to 250 ml. The Group A beakers contained 410 ± 36 larvae and the Group B beakers contained 480 ± 40 larvae each. In each group 6 of the beakers contained a series of dilutions of acetazolamide (Lederle) (see Figure 1) and one containing no acetazolamide was used as a control.

When larvae of *Ostrea lutaria* at the pediveliger stage are released by the female, some setting normally occurs within a few hours (Millar & Hollis, 1963). To reduce environmental variations in this experiment, no cultch shells were added and the larvae set on the walls and bottom of the beakers. After 12 hours any larvae which had not set were removed from the beakers, and the beakers were then rinsed to remove any loosely adhering larvae. The total set per beaker was then counted.

RESULTS AND DISCUSSION

The data are presented in Figure 1. There was a pronounced increase in setting with increasing amounts of added acetazolamide. At an acetazolamide concentration

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of 10^{-4} M the increase in setting for both Group A and B was almost exactly 5-fold. This compares favourably with the highest increases in set accumulation of 5.61-fold obtained by VEITCH & HIDU (1971) using a partially purified proteinaceous "setting factor."

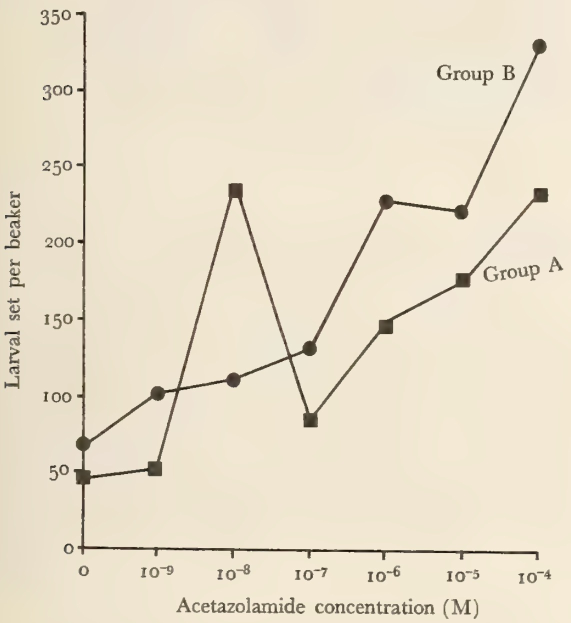

Figure 1

Number of larvae set per beaker versus molarity of acetazolamide

It is not known why there was such a large set in Group A in the beaker containing 10^{-8} M acetazolamide. The setting of oyster larvae is affected by many factors, one of which is gregarious behaviour (which may be related to the previously mentioned "setting factor") (COLE & KNIGHT-JONES, 1949; BAYNE, 1969; HIDU, 1969). It may be that several larvae set prematurely in this beaker, thus precipitating a gregarious setting effect.

The composition of larval cement is not yet fully described and furthermore it is not known whether carbonic anhydrase (CA) is involved in the process of setting. With *Crassostrea virginica*, 1×10^{-9} M acetazolamide causes just less than 50% inhibition of CA activity, and 1×10^{-8} M acetazolamide causes almost complete inhibition (NIELSEN & FRIEDEN, 1972). Therefore it seems unlikely that CA is involved in the process of setting.

The mechanism of action of acetazolamide on the setting of oyster larvae remains to be explained and will be further investigated. It may act directly to induce setting, or it may stimulate the larvae to release the proteinaceous "setting factor" of VEITCH & HIDU (1971). In view of the data of WILBUR & JODREY (1955), it must be pointed out that subsequent rearing of the larvae in the presence of acetazolamide would likely result in retarded shell growth. Therefore acetazolamide should be removed after setting has occurred.

ACKNOWLEDGMENT

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The Neuroanatomy of the Osphradium in *Conus flavidus* Lamarck

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(2 Plates; 1 Text figure)

INTRODUCTION

STUDIES OF THE MOLLUSCAN OSPHRADIUM from the physiological, behavioural or anatomical viewpoint have shown this organ to be complex in nature and enigmatic in function. There is good evidence to show that the osphradium is a receptor but its precise functions remain a matter for some speculation.

Physiological studies have been carried out by a number of workers; for instance, BAILEY & LAVERACK (1966) examined the central responses to osphradium stimulation in *Buccinum undatum* Linnaeus, 1758 whilst STINNAKRE & TAUC (1969) studied the properties of an osmoreceptor in the osphradia of several species of *Aplysia* Linnaeus, 1767. Behavioural analysis of *Bullia laevissima* Gmelin, 1791 by BROWN & NOBLE (1960) showed that extirpation of the osphradium abolished the food detection capacity of the animal.

Recent anatomical work has shown that the osphradium of *Buccinum undatum* and *Neptunea antiqua* (Linnaeus, 1758) has at least 5 sensory cell types possibly associated with chemosensation and vibration perception (WELSCH & STORCH, 1969). A light microscope study of the osphradial lamellae in *Conus flavidus* Lamarck, 1810 (ALEXANDER, 1970) identified sensory cells which seem to correspond to the type 2 cells described by WELSCH & STORCH, (*op. cit.*)

The central axis of the osphradium of those forms possessing a bipectinate osphradium has, however, received little attention. This axis is usually referred to as an osphradial ganglion and is stated to contain many ganglion cells and nerve fibres. KOHN (1961) shows a section of the osphradium of *Busycon canaliculatum* (Linnaeus, 1758) with centrally placed longitudinal fibres in the axis together with groups of nerve cells peripherally.

The present study revealed a very complex organisation of nerve fibre pathways which were disclosed by transverse and longitudinal serial sections. The essential features of the organisation are described together with some comments on the possible reasons for such complexity.

MATERIAL AND METHODS

Specimens of *Conus flavidus* were obtained from the Great Barrier Reef off Cairns, Queensland, Australia and air freighted to Townsville. The animals were kept in tanks of circulating sea water for several weeks and were not fed.

Explanation of Figures *2* to *6*

Figure *2*: Superficial fibres found in level I. One of the lateral tracts and 4 of the transverse fibre bundles can be seen

Figure *3*: The complex fibre pathways typical of levels III and V. Parts of the lateral and median tracts and many transverse bundles can be identified

Figure *4*A: Detail of the fibre bundles in level III. Figure *4*A shows bundles of fibres originating in a lamella which appear to enter the median tract initially and then recurve into the lateral region ipsilaterally before crossing to the opposite side of the axis. Figure *4*B shows a bundle of fibres apparently connecting adjacent lamellae

Figure *5*: Nerve branches leaving the base of the osphradial axis photographed through the mantle wall

Figure *6*: The group of nerve cells buried in the mantle tissue adjacent to the osphradium

Figure 2 100μ

Figure 3 100μ

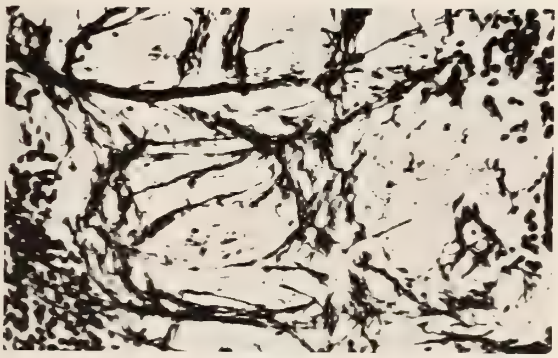

Figure 4 a 10μ

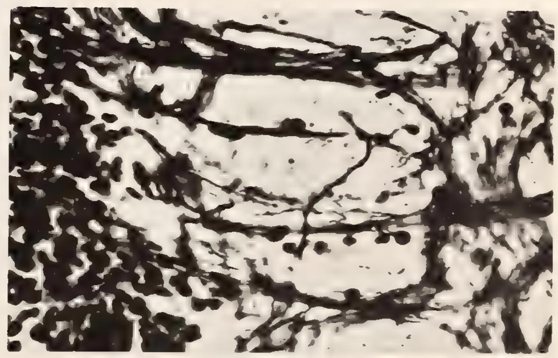

Figure 4 b 10μ

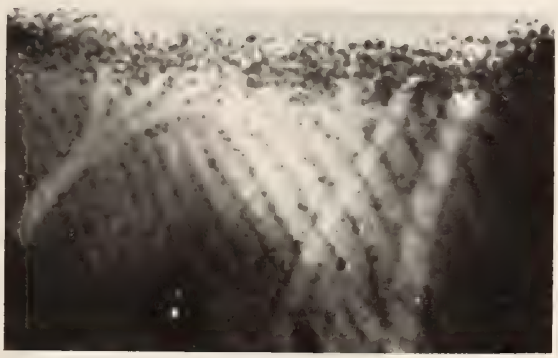

Figure 5 0.5 mm

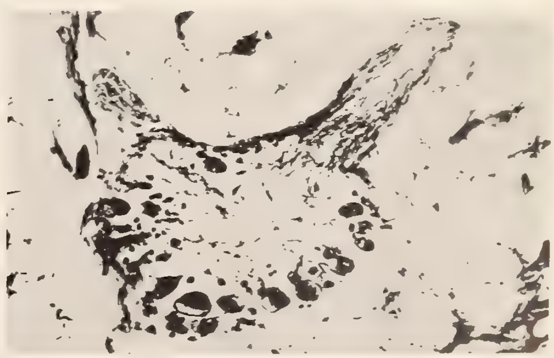

Figure 6 100μ

For histological studies of the osphradial axis, the whole osphradium and ctenidium together with an extensive area of mantle were removed. This enabled associated structures to be examined and also allowed the organ to be pinned out on a cork base and thus remain flat during fixation and subsequent dehydration. Despite these precautions it was not possible to obtain a perfectly flat preparation of the whole organ. Sections were fixed in Bouins fluid or Cetyl pyridinium chloride and formalin (PEARCE, 1968) and embedded in Paraplast. Serial 15μm horizontal sections through the whole structure and serial 10μm transverse sections through representative portions were taken. It was found that 10μm sections revealed the fibre configuration in TS more clearly than the thicker sections.

The sections were stained by Bodian's method (1936) using a 0.5% solution of Protargol S (Winthrop Laboratories, N. Y.) without metallic copper. After examination, representative sections were photographed with a Carl Zeiss photomicroscope II.

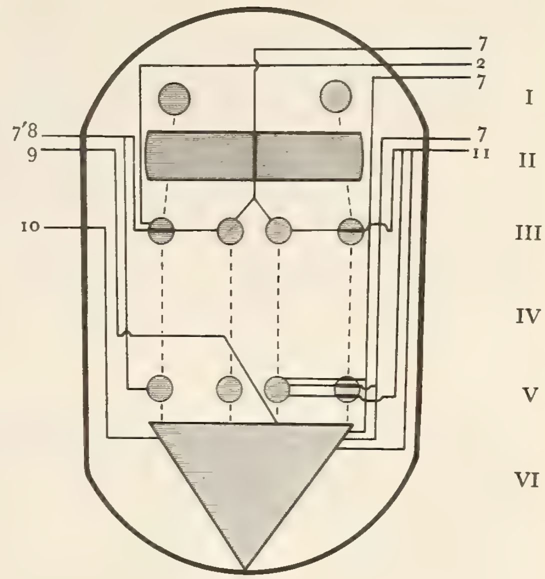

Figure 1

Diagrammatic transverse section of the osphradial axis in *Conus flavidus*. The stippled areas indicate the position of the levels I to VI. The numerals refer to the micrographs Figures *2* and *7* to *11* which show some of the nerve fibre pathways revealed by silver staining

RESULTS

(a) Horizontal organisation

From a number of serial section preparations it has been found that the total depth of the osphradial axis in *Conus flavidus* is about 0.5 mm. Because of the slight wrinkling effect, it proved impossible to obtain perfectly horizontal longitudinal sections along the whole length of the organ. Accordingly, each individual section in a series showed a regular horizontal pattern of structures derived from different levels in the axis. It was, however, possible to reconstruct the pattern of fibre organisation within the axis. This was done by examining the structure at a number of fixed points on each successive section from the dorsal to the ventral surface of the axis.

There are gross differences in organisation at various depths in this axis and these will be referred to as levels. The six apparently distinct levels are described below and their relative positions summarised in the diagram (Figure 1).

Level I

This is the dorsal region immediately below the superficial epithelium and is about 20μm in depth. Lateral tracts are present with transverse fibres, originating in the lamellae, running immediately below them (Figure *2*). The transverse fibres run downwards in the peripheral region opposite their point of entry and appear to terminate in level III (Figure 1).

Level II

This region is approximately 50μm in depth. Dorsally there are a large number of longitudinally orientated fibres. Towards the base of this level, these fibres begin to separate into 3 distinct tracts, a median and two laterals.

Level III

This is evidently a region of major information exchange. The 3 distinct tracts seen at the base of the preceding level are now very obvious and remain thus for a total depth of about 80μm. The median tract has a double configuration and there is clear evidence of fibre decussation (Figure *3*). Large fibre bundles enter the axis at this level from the lamellae and join the median tract. It is probable that some fibres enter the median tract only to disengage to another lamella ipsi or contralaterally but there is no way to show this conclusively using the present methods. Figures *4*A and *4*B show details of lamellar fibre bundles entering the median tract only to recurve into the lateral and a group of fibres which seem to connect two adjacent lamellae.

Level IV

This area, which extends for $150\mu m$, has very few horizontally running fibres. The well defined tracts found in the preceding level are absent. The only identifiable fibres in horizontal section are a few scattered transverse fibres although there is no input from the lamellae. In this region the fibres run vertically in the axis, a feature confirmed by transverse sections.

Level V

This is another region of complex fibre pathways similar to level III but not so extensive in depth (about $50\mu m$). There is a well developed median tract having a double configuration and which appears to receive transverse fibres from both sides of the axis. There is no direct connection with the lamellae at this level; lamellar fibres which enter at higher levels descend to this region in the lateral walls of the axis.

Level VI

The start of this region is taken to be the point where the large median tract seen in the preceding layer disappears. There is no direct input from the lamellae but there are a large number of transverse fibres. The whole level is about $60\mu m$ deep and is marked by the large number of fibres running vertically from the dorsal regions and by the gradual coalescence of the fibres into a basal tract from which a total of 12 nerve branches are tapped off. These nerves (Figure 5) run to a small region of nerve cells buried in the mantle tissue to the right and to the anterior of the osphradium. In section this region is about 0.5 mm in diameter and buried in the mantle wall. For these reasons it has not been possible to locate this structure by dissection even after carefully following the basal nerves stained with methylene blue. The appearance of these cells in section is shown in Figure 6. From here, the osphradial nerves begin their course to the brain.

(b) Vertical organisation

The basic level structure revealed by horizontal sectioning was confirmed in vertical sections.

There is considerable vertical communication between the various levels in the axis. Fibres entering the lamella can either run directly to a major tract at that level, *e. g.* I or III, or run down to one or more levels. This considerably complicates the whole organisation.

A number of identifiable pathways have been observed which are represented diagrammatically in Figure 1. It is assumed that the physiological and anatomical trend of all sensory fibres in this organ is from dorsal to ventral because the nerves which leave the osphradium do so from the base of the organ. In Figure 1, the Roman numerals refer to the level whilst the Arabic numerals refer to the photo-micrographs.

DISCUSSION

The most noteworthy features of the structure of the osphradial axis are the large number and complex pattern of nerve fibres and the apparent complete absence of nerve cells. By definition a ganglion is a discrete collection of nerve cells, so the nervous tissue within the central axis of the osphradium in *Conus flavidus* cannot be called a ganglion. It is therefore proposed to name this the osphradial plexus, signifying a web or meshwork of fibres. A plexus may or may not have nerve cell bodies associated with it but in this case is a more accurate description than the term ganglion.

There is little information in the literature to describe the osphradial axis of other gastropods. Dakin (1912) shows no detail of the "ganglion" in *Buccinum undatum* but concentrates on the leaflets or lamellae. Yonge (1947) does not mention the presence of cells in the osphradial "nerve" of either *Buccinum* or *Neptunea*. Kohn (1961) figures a section of the osphradium of *Busycon canaliculatum* which shows fibres centrally in the axis and cells peripherally although both these features are very difficult to distinguish in the plate. Such cells are not apparent in *Conus flavidus*. Darkly staining bodies occur peripherally in the axis of *C. flavidus* and are abundant in the dorsal regions. These are epithelial and connective tissue cell nuclei preferentially stained by the silver protein. There is no evidence of cells with the typical prolongations of a neuron. In *C. flavidus* the neurons associated with the osphradium lie to the right anterior of the organ, embedded in the mantle tissue. This patch of cells is probably the actual osphradial ganglion and contains between 15 and 20 nerve cells, each approximately $20\mu m$ in diameter.

Three regions in the plexus show clear connections with the lamellae; these are at levels I, II, and III. Some

Explanation of Figures *7* to *11*

nerve fibre pathways seen in the osphradial axis. Stain, Bodian Protargol S. Measure = 100μ

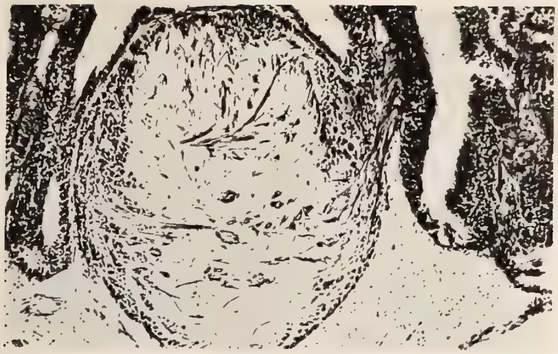

Figure 7 100μ

Figure 8 100μ

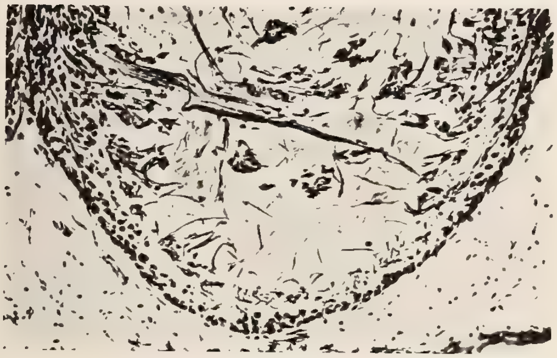

Figure 9 100μ

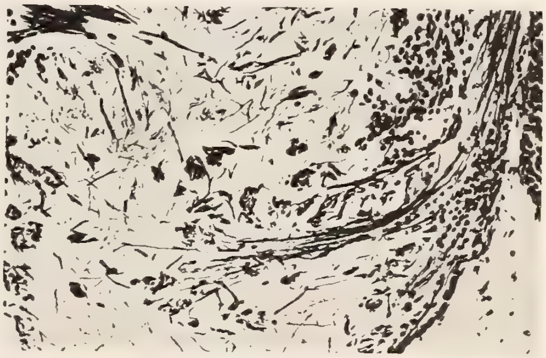

Figure 10 100μ

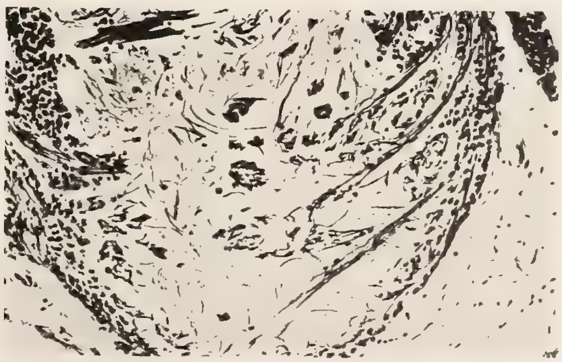

Figure 11 100μ

fibres have been traced in level III which clearly show that a bundle of fibres leaves a lamella and enters the median tract. It may either remain as part of that tract or diverge from it and enter another, ipsi or contralaterally. There seems to be direct contact between the lamellae and this may represent some form of reflex arc. It has been observed that a stimulating chemical introduced anteriorly activates the whole osphradium within one or two seconds, much faster than the current of fluid could be passed along the organ by ciliary action. It is therefore suggested that the whole organ may be brought into a state of readiness to receive a chemical stimulus and thereby obtain the maximum information from a given quantity of stimulus. It is possible that the looping fibre tracts seen in level III are involved in rapid conduction of impulses from the site of initial stimulation to the contractile elements of the lamellae along the entire length of the osphradium. It also seems probable that there are special cells in the lamellae whose function it is to relay this information to the contractile elements of successive lamellae. These cells have not been identified in light micrographs but WELSCH & STORCH (1969) found 5 sensory cell types in their electron micrographs; some may be special mechanoreceptors which facilitate rapid arousal of the whole organ as soon as the stimulus is received.

The neurons associated with the osphradium found in histological section, but not in dissection, may be the centre for initial integration and inhibition before sensory information is passed to the brain for analysis. The presence of this ganglion probably explains why it has proved difficult to obtain meaningful extracellular recordings from the osphradial nerve in response to chemical stimulation of the osphradium. The initial signals appear so modified that the impulse patterns seem not to be correlated with the applied stimulus. The solution to the problem of recording primary sensory activity from this organ in *Conus* may lie in the small basal nerves which are possibly large enough for extracellular recording.

It has been possible to obtain some preliminary oscillograph records from the osphradium by using a glass capillary suction electrode inserted into the base of the osphradial axis. This can be done by making a tiny puncture in the mantle tissue overlying the axis and positioning the electrode tip over it. The activity recorded showed bursts of activity at intervals of between 2 and 3 minutes with intermediate periods of quiescence. The activity is compound in nature and each burst lasts for about 20 seconds. It is thought that this activity reflects a scanning mechanism, part of which is derived from movement of the siphon which does move from side to side at fairly regular intervals. It is evident that the activity is partly motor and partly sensory in character. The effect of dissolved compounds, which could be stimulants, is now being investigated electrophysiologically.

SUMMARY

The central axis of the osphradium in *Conus flavidus* contains a complex of nerve fibres revealed by silver staining. Six distinct levels of organisation have been found. It appears that there are no neurons present within the osphradial axis in this species, so the term osphradial plexus is proposed for this structure. A group of small neurons closely associated with the osphradium may be the true osphradial ganglion.

ACKNOWLEDGMENTS

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Intraspecific Trail-Following in the Marsh Periwinkle *Littorina irrorata* Say

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

OBSERVATIONS OF A COMMON marsh snail, *Littorina irrorata* (Say, 1822), along the shore line of Old Tampa Bay (Tampa Bay), Florida, indicated that many snails that encountered a trail made by another of the same species, followed on that trail and usually in the direction (with the polarity) taken by the snail that secreted it (Figure *1*).

This report presents results of experiments designed to determine if intraspecific trail-following is a characteristic behavior, if snails preferentially follow trails with or against the trail's polarity, if the pattern is related to sex or the angle at which a snail encounters the pathway, or the direction, right or left, that a snail must turn to follow with or against the polarity, and if light or compass direction affect following.

MATERIALS AND METHODS

A collection of snails was separated by sex. Males have a penis on the right side of the head shortly behind the right tentacle. The organ is observable in males of shell length greater than 6mm (BINGHAM, 1969), and all snails tested had shell lengths greater than 10mm. Several 6×10cm strips of crepe surface, neutral pH, filter paper were placed on a clean glass plate and sprayed lightly with synthetic seawater to approximate moisture of the natural mudflat habitat. The plate was inclined to 30° from horizontal and a trailmaker snail was placed at the base of each strip. The trailmaker generally crawled upward on the filter paper producing a straight or slightly curved trail. The trailmaker was discarded, and the strip was immediately transferred with forceps to an observation stage consisting of a glass plate that had a 25cm circle drawn on the underside (Figure 2). The circle was divided into 16 equal sectors (0 - 15), and sequence of numbers from 0 to 15 was drawn from a random numbers table. The transferred trails were laid on the sectors with the polarity running from the center of the circle to the perimeter and thus had no consistent compass direction relative to the observer or the laboratory. All experiments were run in diffuse overhead fluorescent illumination to minimize cues from light.

Two potential followers were placed on opposite sides of each trail and each within 2cm of a different portion of the trail and at right angles to it (Figure 2). By starting snails on opposite sides, preferences for right or left turns could be detected. A snail's recognition of the trail was indicated by increased activity of its snout and tentacles. About 5% of the snails were non-reactive, remaining withdrawn in their shells and never discovering, or not following trails when they encountered them. The analysis, however, was limited to snails that followed trails. No snail was used more than once either in trail making or following. If the snail crawled a minimum distance of 3cm with the polarity, the performance was scored (+). Following against polarity was scored (—). Four possible combinations of followers and trailmakers (male intercepting a female trail, male - male, female - male, and female - female) were tested.

As the snails proceded with or against the trail's polarity, results were plotted on a sequential analysis design described by COLE (1962). The null hypothesis tested was that there was no preferential following in or against the direction taken by the trailmaker. Performances were plotted into 3 areas of decision: (1) preferential following against polarity; (2) preferential following with the polarity; and (3) no significant preference of direction. As soon as performances entered an area of decision, the trials were terminated.

1 cm

Figure *1*

Littorina irrorata following an intraspecific trail

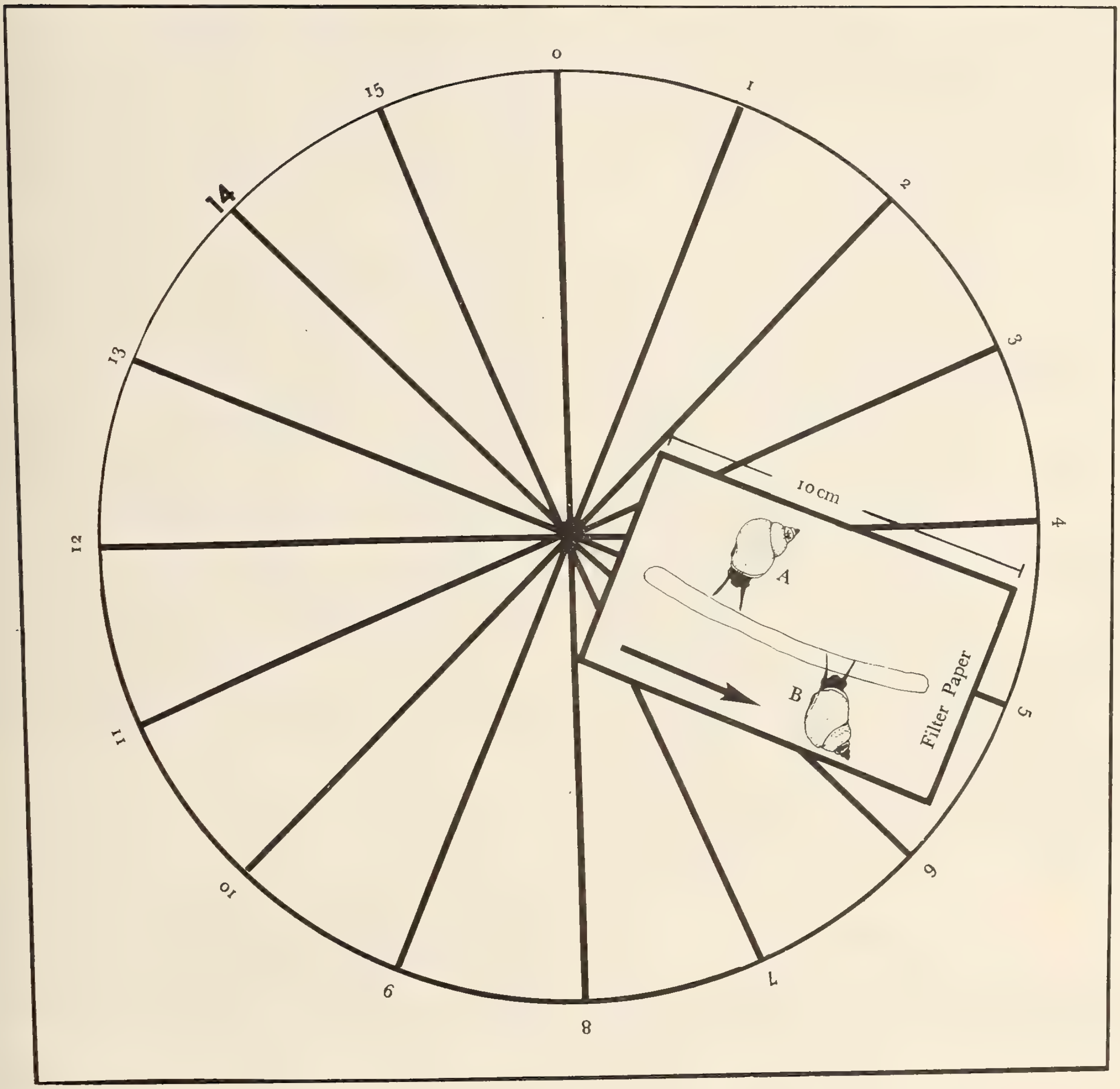

Figure 2

Diagram of observation stage showing *Littorina irrorata* encountering an intraspecific trail on filter paper. The arrow indicates the polarity of the trail, which in this case was along sector 5. Snail A was placed so that it must make a left turn to follow the polarity; Snail B must make a right turn

RESULTS

In the experiments, once a potential follower contacted a trail, it would consistently maneuver so that it was almost exactly perpendicular to the trail, no matter what the initial angle of contact was. Thus the angle of interception appears to be unimportant. After this orientation, the snail would place its snout onto the trail, and its tentacles would tap on positions of the trail about 1 cm apart.

In the first trials, males preferentially followed the direction taken by females (Table 1). Fourteen of 17 snails placed so that they had to make a right turn to follow with polarity (Figure 2, snail B) made the right turn and followed the trailmaker's direction. Plotting results by "left turners" (snail A) produced preference of following polarity after 28 trials.

Similarly, in the second set of experiments, males preferentially followed polarity of trails made by other males whether the correct turn was a right or left hand decision.

A new collection of snails was made for the third and fourth set of trials – females intercepting male and female trails. Results were similar to the first two sets of trials.

Inspection of results indicates no clear preference for either a left or right turning direction or any compass direction. Furthermore, the snails on the stage showed no observable visual response to each other. Subsequent experiments were later performed using a single potential follower to intercept a trail (R. Orlopp and J. Floyd, University of South Florida, Department of Biology, Tampa, Florida 33620, personal communication). Results from these trials showed significant following of polarity and confirmed that snails respond only to the trails and not to each other.

DISCUSSION

Trail following is an activity that is infrequently reported in marine invertebrates. Tactile and olfactory capacities of the cephalic tentacles of *Littorina littorea* (Linnaeus, 1758) were reported by Fretter & Graham (1962), and it is probable that *L. irrorata* is using these sensory capacities. The approximately 1-cm spread between reception points on the snail's tentacles may provide the comparative sampling leading to the decisions and preferences shown in this report. Peters (1964) found that cephalic tentacles of *Littorina planaxis* (Philippi, 1847) were important for tactile surveillance of the substratum, used in sex recognition, and were employed in following inter- and intraspecific mucous trails, but gave no indication of the snail's ability to recognize or follow the polarity of trails. Moulton (1962) found clustering in an Australian cerithid mediated by its ability to follow intraspecific slime trails. A molluscan predator, *Natica (Natica) chemnitzii* Pfeiffer, 1840, followed a trail to its prey, *Nassarius (Arcualia) luteostoma* (Broderip & Sowerby, 1829), but successful capture was apparently dependent on accidental choice of direction of pursuit (Gonor, 1965). Similar behavior was reported by Simon (1965) in two polychaetous annelids, in which the predator, *Eteone heteropoda* Hartman, 1951, pursued and attacked *Nereis succinea* (Frey & Leukart, 1847).

Male or female *Littorina irrorata* may exhibit an ability to track down opposites of the same species if they were actively seeking each other for reproductive purposes. But experimental results indicate that individuals of both sexes detect and follow the path in the direction taken by either sex. This was commonly seen in the field when

Table 1

Following of intraspecific trails by *Littorina irrorata*. Trail sectors are any of sixteen random numbers (0 - 15). Right and left indicate the turn the intercepting snail must make to follow with the polarity of the trail. A (+) indicates that the trail was followed with the polarity; a (—), that it was not.

Male	Trail Sector	7	4	5	7	14	2	8	8	2	1	9	13	10
intercepting	Right	+	+	+	+	+	—	+	+	—	+	+	+	—
female trail	Left	+	+	—	—	+	+	—	+	+	—	+	+	+
Male	Trail Sector	13	4	8	9	2	1	8	14	10	2	15	3	5
intercepting	Right	+	+	+	—	+	—	—	+	+	+	+	+	+
male trail	Left	+	+	+	+	+	—	+	+	+	+			
Female	Trail Sector	4	1	0	2	14	15	14	12	15	12	4	12	4
intercepting	Right	—	—	+	+	+	+	+	+	+	+	+		
male trail	Left	+	—	+	+	+	+	+	+	+	—	+	+	—
Female	Trail Sector	14	1	0	12	4	12	14	2	12	15	13	12	15
intercepting	Right	+	—	+	+	+	+	+	+	+	+			
female trail	Left	+	+	+	—	+	+	+	—	+	+	+	—	+

individuals of either gender, in any sequence, would be seen following on the same trail. A more reasonable explanation for this phenomenon is that such behavior is an energy-saving device. The trailmaker snail expends energy and mucus as it moves across the bay bottom and following snails have a ready-made pathway (Figure *1*). Supportive evidence recorded in the field showed 20 following snails crawling at an average speed of 6.5 cm/min and eventually overtaking 20 trailmaker snails that were moving at an average speed of 4.6 cm/min. Overtaking snails may pass the leader and eventually be overtaken themselves. All trails occur within the intertidal zone and are short-lived; incoming tides or rains disintegrate them. This species also exhibits a disinclination to remain submerged (BINGHAM, 1972), and when wetted by an incoming tide, they climb marsh grass or mangroves until they are clear of the water. They remain there until they become heated by sunlight (BINGHAM, 1969), climb down, make trails, and forage on the bay bottom. Because of this behavior and disintegration of trails, there was no evidence of homing behavior; marked animals dispersed to all parts of the study area.

To my knowledge, this is the first example of an animal choosing to follow the polarity of a trail laid down by a species member based only on initial contact and choice. Factors influencing this behavior such as pheromones (DINTER & MANOS, 1972), the chemical or physical composition of trails, or the occurrence of specific reception or releasing sites on following or trailmaking snails could possibly be demonstrated by further experimentation.

Table 1 [continued]

Following of intraspecific trails by *Littorina irrorata*. Trail sectors are any of sixteen random numbers (0 - 15). Right and left indicate the turn the intercepting snail must make to follow with the polarity of the trail. A (+) indicates that the trail was followed with the polarity; a (—), that it was not.

4	4	5	1	3	6	15	0	1	13	12	14	0	13	5						
+	+	+	+																	
—	+	+	+	+	—	+	+	+	+	+	+	+	+	+						
1	0	4	6																	
+	+	+	+																	
1	13	15	12	13	15	6	10	0	0	10	9	1	5	2	12	12	13	9	11	14
+	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	—	+	+	+
1	4	15	4																	
+	+	+	+																	

ACKNOWLEDGMENTS

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Estimated Growth Functions and Size-Age Relationships of the Hard Clam, *Mercenaria mercenaria*, in the York River, Virginia[1]

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(3 Text figures)

INTRODUCTION

A STUDY OF THE HARD CLAM[2], *Mercenaria mercenaria* (Linnaeus, 1758) resources of Virginia is currently being conducted. One important aspect, their growth in this region, has been limited to the study of small juveniles (HAVEN & ANDREWS, 1957). Our objectives were to demonstrate that *M. mercenaria* growth functions could readily be derived and statistically contrasted, and, subsequently, the age-size relationship could be estimated.

Growth functions in the present study were derived by the Walford transformation (WALFORD, 1946) .The method has been widely used in finfish growth studies but has been applied only to a limited extent in bivalve growth estimates. ANSELL (1968) applied the method to hard clams when he adjusted existing hard clam data from numerous sources to a standard size. His use of the method is dubious, however, since many of the data were from studies in which very limited size ranges were available or chosen. Some of the possible complications arising from the use of restricted size ranges and age groups have been discussed by KOHLER (1963), HANCOCK (1965) and KNIGHT (1968). In addition, to obtain a measure of the instantaneous rate of growth of Virginia hard clams, ANSELL (1968) transformed the data of HAVEN & ANDREWS (1957), and also the North Carolina hard clam data of CHESTNUT, FAHY & PORTER (1957), by using the findings of MENZEL (1963) for similar Milford stock grown in Alligator Harbor, Florida. The validity of the transformation rests upon the assumption of equality of growth rates among sub-groups of a common stock grown in different geographical regions.

This report does not review the extensive literature on hard clam growth. However, past investigators, in general, were concerned with comparative growth rates over relatively short periods of time. A selected size group was generally used, and, moreover, some investigators confined their experimental units to trays or sediment boxes for the duration of their experiments. Under the latter condition, growth rate estimates for wild populations in natural substrates were precluded even though the trays were filled with substrate common to the area.

HASKIN (1949, 1952 and 1954) graphically presented curves for the first 8 to 10 years of *Mercenaria mercenaria* growth derived from average weight increments to arbitrary size intervals. While one might concede that large estimated differences among locations or years were real, his presentation did not allow for statistical analysis of lesser differences.

MATERIALS AND METHODS

The annual increment to shell length, where length is defined as the longest linear dimension, was used to estimate growth.

Hard clams from the smallest size practical for marking through the larger sizes (approximately 30 to 90mm) were measured, code-marked, and planted in the substrate. Clams were marked initially with a Mark-Tex-Tech-Pen and enamel but an indelible Felt Riter pen was later employed. Code marks were applied more readily with the latter pen, dried faster, and have persisted up-

[1] Contribution No. 497 from the Virginia Institute of Marine Science, Gloucester Point, Virginia 23062

[2] The term 'hard clam' is used as a synonym for *Mercenaria mercenaria* in this paper

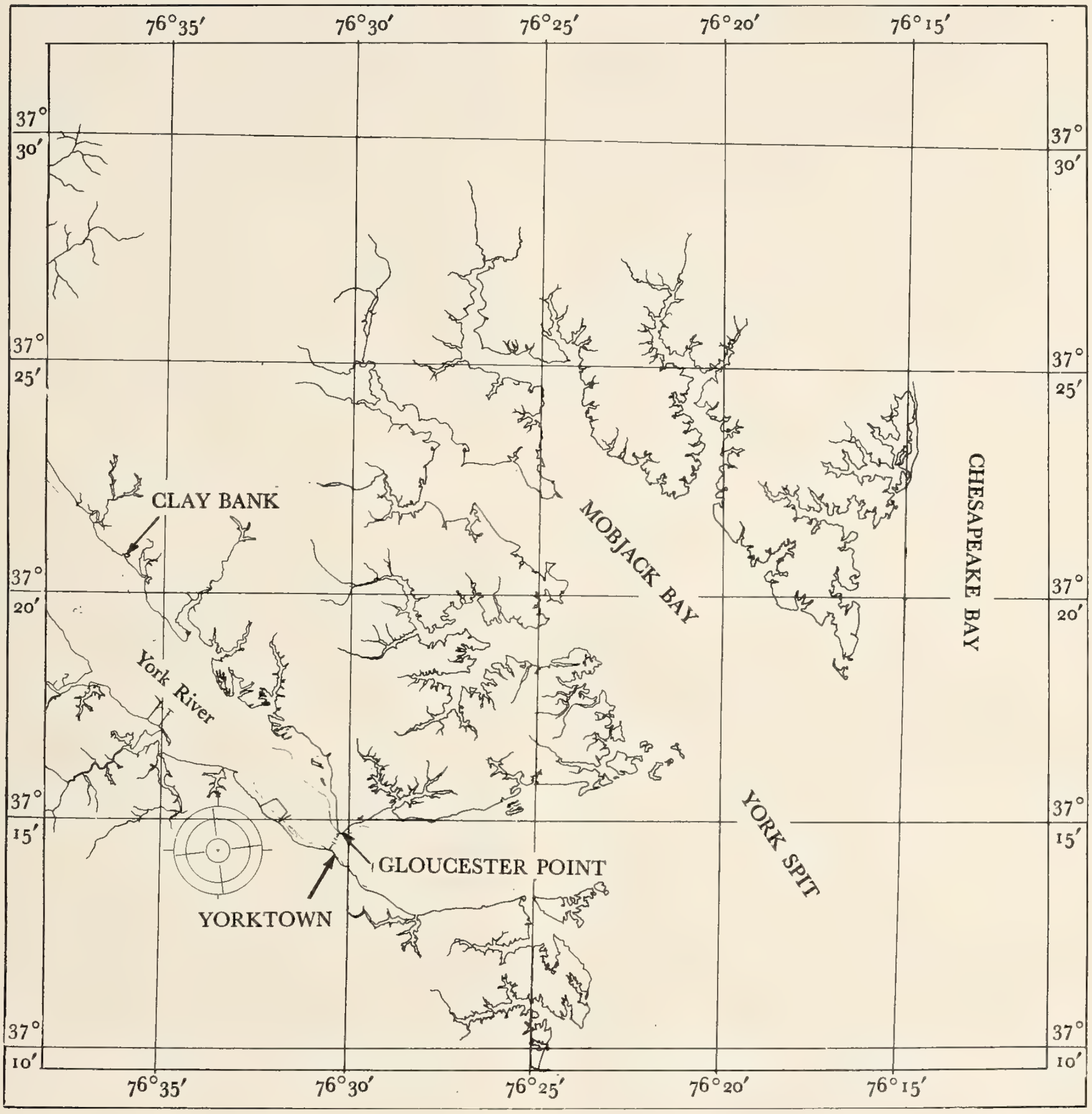

Figure 1

Locations of the experimental plots (Gloucester Point and Yorktown), source of the hard clams (York Spit) and the limit of their upriver distribution (Clay Bank)

wards of three years. An experimental plot was established in the York River adjacent to the Virginia Institute of Marine Science laboratory at Gloucester Point in mid-September, 1967 and another plot was established near the opposite shore at Yorktown, Virginia in mid-November, 1968 (Figure 1). The two groups were formed from native stock obtained from the York Spit area at the mouth of the York River. SCUBA was used for the placement and recovery of the hard clams. After recovery at approximately yearly intervals, the hard clams were measured to the nearest 0.1 mm and replanted. Salinity on the Gloucester Point side seasonally ranges from about 19 to 20‰; on the opposite side salinity is generally 1 to 2‰ lower. A sand-mud substrate with scattered shell and

a depth of about 7 feet (MLW) are common to both plots.

Walford (1946) graphically estimated growth parameters from linear expressions obtained by plotting the average length of known age groups against the average length of the next youngest age group. His coordinates, therefore, were derived from different groups. In the present study, coordinates were determined for each individual clam and yearly growth expressions derived by the method of least squares. Manser & Taylor (1947) first employed individual measurements to graphically estimate the rate of growth of English sole, *Parophrys vetulus* Girard, 1854, while Linder (1953) utilized growth increments in the shrimp, *Penaeus setiferus* (Linnaeus, 1767), to demonstrate the applicability of least squares.

The derived expressions have the general linear form:

$$Y = a + bX$$

but following the more definite notation of Ricker (1958) this becomes:

$$l_{t+1} = l_\infty (1-k) + kl_t$$

Here, $X = l_t$, the length at time t; $Y = l_{t+1}$, the length at the end of a constant time interval (one year in this study); $a = l_\infty (1-k)$, the Y-intercept from which l_∞, the **average** maximum or asymptotic size, can be estimated, and $b = k$, the slope of the Walford regression line. Asymptotic size may also be graphically estimated from the intersection of the regression line and a 45° line; further, it is the "nature" of k that the smaller its value, the greater the rate at which l_∞ is approached (cf. Walford, 1946).

Growth functions are often expressed in terms of the growth equation presented by von Bertalanffy (1938), in which asymptotic size is but one parameter. The asymptotic size derived by the Walford line is generally a preliminary estimate and may be modified (cf. Beverton, 1954; Ricker, 1958). Modification requires an independent estimate of the length-age relationship, as for example, that obtained from back calculations of growth obtained from fish scales. In the present situation with hard clams, lacking the independent estimate, the Walford regression line was employed without modification.

The Walford transformation can be used to estimate growth independently of age. Subsequently, the average size of at least one age group must be known in order to relate size to age. To estimate this relationship two methods were employed. First, young clams spawned at this laboratory were planted in sediment trays and, in turn, the trays were placed in the York River substrate adjacent to the laboratory. These clams were too small (approximately 5 mm) to be marked individually, therefore, the average size of clams in replicate trays was recorded at yearly intervals for three years. The second method was based upon observations at this laboratory, and previously reported by Loosanoff, Davis & Chanley (1966), that hard clams at age zero, the time when the larvae settle to become part of the benthic community, are about 210 µm in length. The value was substituted into the derived growth function to obtain an estimate of length at age one, age one size was then substituted into the equation to estimate size at age two, and so on. It was assumed that clam spat growth is post-inflection-point with respect to an asymmetrical sigmoidal growth curve.

Regression lines were analyzed by covariance and significance is reported in terms of the probability (P) due to chance of obtaining a deviation $\geqslant$ that observed.

RESULTS AND DISCUSSION

Estimated growth functions are presented in Table 1. Analysis of covariance indicated significant difference among the 5 growth rates ($P < 0.001$). It is obvious by inspection that the 1968-69 growth expressions for clams in both locations are similar, and superior to the others. When these data are removed no significant differences could be ascertained among the remaining 3 expressions ($P > 0.75$ for both the estimated growth rates and the adjusted means). Similarly, no significant difference could be detected between the two growth expressions for the 1968-69 growth year ($P > 0.05$). Thus, it appears that growth in the observed yearly intervals did not vary between the two locations, but environmental conditions for growth were more favorable during the 1968-69 period. Estimates of asymptotic size ranged from 79 to 82 mm. This variation may be sampling error because it is not associated with a given plot location or growth year.

Table 1

Estimated Growth Equations for Hard Clams in Two York River Experimental Plots

Plot Location	Growth Year	Number of clams	Growth Functions	Asymptotic Size (mm)
Gloucester Point	1967-68	187	$Y = 12.1 + 0.848X$	80
	1968-69	117	$Y = 19.2 + 0.762X$	81
	1969-70	302	$Y = 12.6 + 0.846X$	82
Yorktown	1968-69	156	$Y = 18.2 + 0.770X$	79
	1969-70	144	$Y = 12.1 + 0.852X$	82

The separate growth functions discussed above were suitable for comparing growth between experimental plots and among years. An estimate of the "average" growth function derived from the pooled data of the growth years common to both plots is shown in Figure 2.

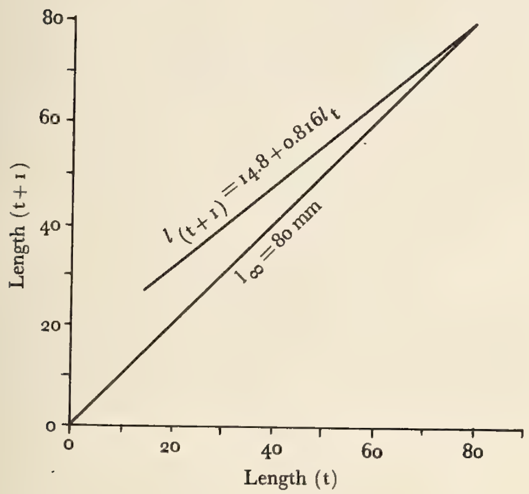

Figure 2

Estimated growth equation derived from the pooled data for the 1968-69 and 1969-70 growth years

The age-length relationship was determined by substituting age zero length, 0.21 mm, into the common growth function (Table 2). The estimate of age one size obtained from clams in sediment trays was not used because of suspected stunting. Average one-year-old sizes attained in 5 trays used over 3 years ranged from 7.8 to 11.7 mm with an overall average of 8.7 mm. This value is only 58% of the predicted one-year-old mean size of 15 mm derived from the growth function. Growth data of two-year-old clams in trays were ambiguous; clams in 3 trays averaged 25.9 mm when the densities were only 12, 15 and 29 clams per tray; however, 200 clams in a fourth tray exhibited no average length increment between the first and second years. Recent growth data (unpublished) of young hard clams in a gravel substrate at Gloucester Point also indicate that the 8.7 mm is an unrealistically low estimate of one-year-old length. Menzel (personal communication) noted retarded growth when young clams were retained in sediment filled trays and transplanted the clams to a natural bottom when they were about 25 mm in length (Menzel, 1963).

An asymptotic size of 80 mm was estimated from the pooled data. This relatively low value may reflect the limited number of observational years, the use of age zero length, or the inability to adjust the asymptotic estimate. Sampling of hard clams in relatively shoal depths similar to the experimental plots (about 5 to 10 feeet MLW) in the lower-and-upper part of their York River range, however, indicated that a small maximum size is attained because the clams tend to blunt. Blunting is defined as a form of stunting in which the free edges of the valves, the ventral margin, thicken and recurve inward. Observations of marked blunted hard clams indicated that growth in length ceases and in some individuals length may decrease; Saloman & Taylor (1969) reported this phenomenon for *Mercenaria campechiensis* (Gmelin, 1791). Blunted clams comprised 37.9% of 1 016 clams in 7 samples taken between Yorktown and Clay Bank (Figure 1). In contrast, in 2 shoal-water samples each at Poquoson and Hampton Flats outside the mouth of the York River only 4 of 502 clams (0.8%) were blunted. There were intergrades between sharp-edge and blunt-edge clams but only those having the entire ventral margin affected were designated as blunt clams and the above percentages are minimal. The potential stunting effects of a limited food supply and unfavorable conditions of salinity, temperature, oxygen, turbidity and other factors upon aquatic organisms have been reviewed by Hallam (1965). Environmental factors were not monitored in the present study but relatively low salinity in these shoal water experimental sites is suspect as a major limiting growth factor.

Longevity of hard clams is not definitely known. Estimates based on counts of growth rings range from 25 years (Kerswill, 1941) to as high as possibly 40 years (Hopkins, 1930). In general, determining age from growth rings is unreliable, particularly in older hard clams, when rings produced by environmental and physiological changes are not recognized. This has been confirmed by microscopic investigation of transverse shell sections by Pannella & MacClintock (1968) and Rhoads & Pannella (1970).

The asymptotic size based on the present estimated growth rate would not be reached until age 22 (Table 2). This estimate of late attainment of the average maximum size is probably the result of an antagonistic interaction between inherent growth potential and the tendency to blunt. Growth ceases, for all practical purposes, at about age 14 or 15; after this the predicted annual increments are less than 1 mm. Of more importance is the estimate that the young hard clams in this area would not attain Littleneck size until age 4 and Cherrystone size until age 8 (based on local market size definitions). At these ages

Table 2

Estimated Age - Length Relationship for Hard Clams in the Gloucester Point and Yorktown Experimental Plots, derived from the pooled data of the 1968-69 and 1969-70 growth years

Age (Years)	Length (mm)	Age (Years)	Length (mm)	Age (Years)	Length (mm)
1	15	9	68	16	77
2	27	10	70	17	78
3	37	11	72	18	78
4	45	12	73	19	79
5	51	13	75	20	79
6	57	14	76	21	79
7	61	15	77	22	80
8	65				

the hard clams attain about 56 and 81% of their asymptotic size, respectively.

Haven & Andrews (1957) reported that 25 young *Mercenaria mercenaria* held in a suspended sediment tray for 2 years, and others of this group placed in the natural substrate for the second year, attained average lengths of 37 mm and 33 mm, respectively. These observed lengths exceed the estimated length of 27 mm for two-year-old hard clams in the present study. The initial average length of their young hard clams, however, was 11 mm, which is 52 times greater than the initial length (0.21 mm) substituted into this study's derived growth function. The 11 mm length is 73% of the predicted length increment from age zero to age one. A more realistic comparison, therefore, is to contrast the lengths observed by Haven & Andrews (1957) with the predicted length derived from the cumulative growth curve (Figure 3) for approximately a $2\frac{3}{4}$ year old clam in the present study. The latter length is approximately 34 mm, and in agreement with the length observed by Haven & Andrews (*op. cit.*).

In summary, the Walford transformation can readily be applied to statistically contrast relative growth among areas and years for hard clams. Derived estimates of the age-size relationship appear reasonable but should be substantiated by microscopic studies of transverse shell sections or by following the growth of young individuals of known age through several growth years.

Figure 3

Cumulative growth curve

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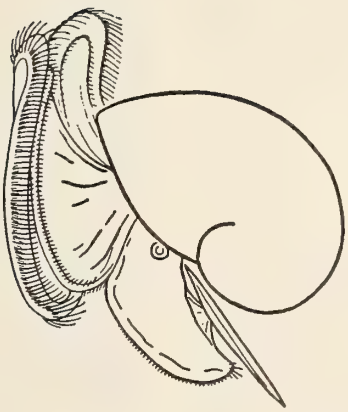

Some Aspects of the Biology of *Terebra dislocata* Say, 1822

(Gastropoda : Prosobranchia)

BY

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INTRODUCTION

Terebra dislocata Say, 1822 is a common gastropod in the area of Beaufort, North Carolina, where it is found in quantity in the tidal pools on exposed sand flats. The range of the species extends from Virginia to Texas and the Virgin Islands; the species is perhaps most abundant in Florida (Morris, 1960). The animals are often found at the head of a V-shaped furrow they leave behind, or in the castings left by the hemichordate *Balanoglossus aurantiacus* (Girard, 1853). The shell of *T. dislocata* is a grayish brown or yellowish white, $2\frac{1}{2}$ to 5 cm in length, with a surface sculptured by wavy longitudinal folds and spiral grooves.

Despite the ready availability for study of this species, a search of the literature uncovered no references dealing with the biology of this gastropod. This paper seeks to present preliminary information on several aspects of the biology of *Terebra dislocata*. Future studies of a more specific nature will hopefully answer some of the questions raised.

LOCOMOTION

Probably as a result of the length of the shell, *Terebra dislocata* drag it behind them as they move. Usually they travel buried just below the sand surface with the siphon extended into the overlying water, but they may be found also at the surface. The broad foot apparently has a direct, monotactic movement which is continuous, whereas the shell is moved discontinuously. Increased tension on the pedal retractor muscles, caused by shell drag, evidently must stimulate them to pull the shell forward. The shell is supported by the substrate during horizontal movement, even on glass. However, *T. dislocata* are apparently not able to furnish the torque necessary to lift the long shell over an edge, and they therefore seldom escape from open glass containers.

FOOD HABITS

Examination of the stomachs of 35 specimens gathered in the sand flats near Beaufort in August of 1971 and preserved in the field failed to uncover a single food particle. The Terebridae are commonly thought to have poison glands and a radula (Kaestner, 1967) and are said to be carnivorous in habit, existing on such prey as polychaetes (Hyman, 1967). However, laboratory studies utilizing tissue smashes of the digestive system were unable to detect a radula. In fact, *Terebra dislocata* would not feed in the laboratory when offered a variety of food types, including polychaetes and clam meat. Their common occurrence in the castings of *Balanoglossus* suggests another mode of feeding. It may be that these castings constitute the most concentrated source of organic detritus available on the sand flat surface, and that the snails exploit this food source, which would account for the high degree of association previously mentioned. The absence of carnivorous feeding habits and structures noted may rule out direct feeding upon *Balanoglossus*.

The absence of carnivorous feeding habits and structures is not unusual in the Terebridae. In a discussion comparing 6 terebrid species (*Terebra dislocata* not included), Rudman (1969) found half of them to lack radular teeth and poison glands. He divided the Terebridae into two general groups: those with a foregut similar to cones with poison glands and radulae, and those lacking these structures. *Terebra dislocata* belongs in the second category, but a more thorough examination of feeding structures is necessary in order to ascertain the exact mode of feeding.

REACTIONS TO ENVIRONMENTAL FACTORS

The twice daily tidal exposure of the sand flats subjects *Terebra dislocata* to several possible major changes in

physical environmental factors. The animals may either tolerate or avoid these hardships, and several experiments were designed to determine their reactions to several of these environmental changes.

Light: Because of the burrowing behavior of *Terebra dislocata* it was hypothesized that this species may exhibit an avoidance reaction to light. The following experiment was used to test this hypothesis. A rectangular pan 30cm by 60cm was sprinkled with sand to a depth of 2 cm; water was added to a depth of 3 cm above the sand layer. Ten specimens were placed in an even distribution throughout the pan and half the pan was placed in the shade. At 1½ hour intervals from noon until midnight, the locations of the animals were recorded. The control consisted of a pan arranged as before, but with full illumination. A Chi-square equality analysis ($X^2_{1df} = 6.0$, $p < 0.05$) showed a significant preference for the darkened half of the pan at all hours, while the control distribution did not differ significantly from random expectation ($X^2_{1df} = 0.46$, $p > 0.05$). It is significant that *T. dislocata* did not completely avoid the light, since in nature the animals are found on the surface during the day. However, at night their abundance at the surface is markedly increased. This may indicate that part of the population exploits food resources not available during the night, but no evidence is available to support this hypothesis.

Salinity: Salinity in the tide pools may vary extremely, becoming greater if the water evaporates rapidly, and decreasing if rain dilutes the water in the pools. The reaction of *Terebra dislocata* to decreased salinity was tested by placing 5 specimens in each of five 8½ inch diameter glass bowls which contained sand saturated with 100% seawater. A 3 cm water layer above the sand was diluted with distilled water to 75%, 50%, 25%, and 0% seawater, with 100% seawater serving as a control. All bowls were at room temperature (27° C). The animals in water diluted to 50% seawater or less remained motionless with tightly closed shells. Of the specimens in 75% seawater, one burrowed partially and the others extended their siphons. The specimens in the control group behaved normally, with most burrowing into the sand. All the animals were left at least 8 hours under experimental conditions, and those in 0% seawater were left 12 hours; all survived.

These results indicate that *Terebra dislocata* is not physiologically stressed by reduced salinities at times of low tide even on a rainy day. Behavior was normal at the two higher salinities and *T. dislocata* avoided the lower salinities by retreating into its shell. Avoidance of low salinities could also have been accomplished by burrowing into the saturated sand, but this means of escape was not chosen. However, it may be that the salinity became equalized. Present knowledge of the salinity tolerances of intertidal prosobranchs reveals two basic patterns: a rather narrow tolerance in those existing in areas of stable salinities and a wide tolerance in other groups (Arnold, 1972). Since *T. dislocata* lives in areas where heavy rains may rapidly reduce salinities in tidal pools, it might be placed in the latter group. However, since different populations of the same molluscan species may exhibit strikingly different salinity tolerances dependent upon their location in the intertidal area (Arnold, 1957), further studies are needed in order to determine the specific nature of *T. dislocata*'s salinity tolerances and osmoregulatory ability.

Desiccation: A very low spring tide may leave *Terebra dislocata* stranded outside the usual tidal pools. Their reactions to such conditions were tested by placing 5 specimens in each of three 8½ inch diameter glass bowls containing damp sand, seawater saturated sand, and sand with a 3 cm supernatant seawater layer. To remove the possibility of light avoidance burrowing, the bowls were placed in the shade. After 4 hours, the animals in the first 2 bowls were on the surface extended from their shells, while those in the seawater exhibited normal burrowing behavior. Since other prosobranchs have been known to resist desiccation for weeks or months by tightly closing the operculum (Colgon cited in Newell, 1970), the type of behavior exhibited by *T. dislocata* in the first 2 experimental conditions seems non-adaptive. However, it is not unusual when compared to other gastropods atypically exposed by low tides. Gowanloch (cited in Newell, 1970) reported on the absence of operculum closure in a sublittoral whelk, and Lewis (1964) reported how an upper shore species of *Littorina* closed the operculum while a lower shore species remained extended. These examples illustrate the influence of habitat, and the influence of physiological and behavioral patterns of organisms on their distributions.

SUBSTRATE PREFERENCE

Field observations indicated that adult *Terebra dislocata* were found only within the top sand layer of the Beaufort sand flat, the flat itself being composed of two sand layers (an upper light colored layer approximately 3 cm thick, and a lower one of dark anaerobic sand). An experiment was designed to determine whether the adult animals exhibit a substrate preference resulting in their distribution.

Four substrate types were collected from the field: open beach sand, marsh mud, upper-layer (sand flat) sand, and bottom-layer (sand flat) sand. Each was placed in a 3 cm thick wedge occupying one-fourth the area of a

circular pan 75 cm in diameter. Seawater was slowly introduced in order to prevent disturbance of the substrates, and 6 specimens were placed on each substrate type. Counts of the locations of the animals were made at $1\frac{1}{2}$ hour intervals for a period of 9 hours, ending at midnight. A control consisted of a single substrate type, the top-layer sand, in an identical circular pan. Results showed that about 50% of the animals preferred upper-layer sand, while the others were somewhat evenly distributed on the other substrates. A Chi-square analysis ($X^2_{1df} = 45.0$, $p < 0.05$) showed a significant preference for the upper-layer sand when compared to the other substrate types, while the control distribution did not differ significantly from random expectation ($X^2_{3df} = 1.22$, $p > 0.05$). The specific reasons for the preference have not been determined, but it was not surprising to find a preference for the substrate on which the animals are usually found. The results indicate that all substrates are somewhat acceptable and that other factors may influence distribution more directly, such as oxygen or food availability.

CONCLUSIONS

The above observations and experiments introduce an animal which superficially appears to be well adapted to its environment. The experiments on orientation with respect to environmental variables indicate that its survival is probably not reduced by any one of the factors tested. However, a combination of factors might stress *Terebra dislocata* enough to cause significant mortality. In all areas investigated, further work is necessary in order to ascertain the specific mechanisms behind the behavioral patterns exhibited.

SUMMARY

Terebra dislocata is a common gastropod in the area of Beaufort, North Carolina. Despite its ready availability for research, no references were uncovered which dealt with the biology of this species. Preliminary information on several aspects of the biology of *T. dislocata* is presented.

Examination of the stomachs of 35 specimens failed to uncover a single food item, although the literature suggests a carnivorous feeding habit. Laboratory studies were unsuccessful in revealing a radula, and it was suggested that *Balanoglossus* castings may serve as a food source. *Terebra dislocata* was found to avoid light; it is known to be especially abundant on the sand flats at night. This probably has some ecological significance not yet discovered. Effects of reduced salinities were tested, and specimens of *T. dislocata* were able to avoid the lowest concentrations of seawater by closing their shells. They reacted to desiccation experiments by remaining exposed, which appears to be non-adaptive. However, this type of behavior is not unusual for gastropods atypically exposed at low tides. Substrate preference tests showed that *T. dislocata* clearly preferred the sand type upon which it is normally found. The specific reasons for this preference have yet to be determined.

ACKNOWLEDGMENTS

I would like to thank the Duke University Marine Invertebrate class (Summer 1971) of Dr. Robert Barnes for contributing some data, and Dr. Robert Edwards of Christopher Newport College for reading and criticizing this manuscript.

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An Unusual Habitat for the Rough File Shell, *Lima scabra* (Born, 1780)

BY

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(1 Plate)

On a collecting trip in April 1972 to St. John, United States Virgin Islands, the junior author discovered an unusual habitat for the Rough File Shell, *Lima scabra* (Born, 1780). This nesting species is common under rocks in shallow water (Abbott, 1954: 371), but sometimes, as this report will show, it nests in a different habitat which results in a profound distortion of the shell.

The discovery was made at Mary Point on the northeast coast of the island. The area consists largely of volcanic rock. Next to the shore, the sea bottom drops off sharply to form a terrace at a depth of 15 feet ($4\frac{1}{2}$m), but a narrow rocky beach remains above the high tide level. A fringe of elk-horn and brain coral occurs on the submerged terrace. Lying on the narrow beach were some boulders of brain coral in fresh condition, apparently dislodged and washed ashore during the winter storms. On the underside of these boulders were found burrows of the Giant Date Mussel, *Lithophaga antillarum* (Orbigny, 1846), some of which still contained empty shells. Eight specimens in good condition, a few up to 100 mm long, were taken.

The *Lima* was found imprisoned in one of these burrows (Figure *1*) and since the entrance to the burrow was narrower than the shell, the aperture had to be widened by hacking at the margins before the collector could free the bivalve. The *Lima* is 32 mm wide and 54 mm long, the burrow being 150 or 175 mm deep and only slightly wider than the shell. The burrow was also a little more rounded than the oval burrows in which the *Lithophaga* were found.

The distortion apparently caused by this restricted habitat on the shell of *Lima* consisted of compressing the normally rounded sides of the shell so that it had to assume a quadrilateral outline with almost parallel sides (cf. Figures *2, 3*). It may be supposed that the *Lima,* when still young, entered the burrow and grew there, its increasing size being forced into the distorted shape by the configuration of the *Lithophaga* burrow. If not disturbed, *Lima* can occupy the same nest all its post-larval life (Dennis, *in* Jeffries, 1863: 91). However, if the nest is torn open, the animals are able to swim away rapidly and construct a new burrow when the opportunity is provided (Dennis, *ibid.*: 90; Johnson, 1931: 126; Gilmour, 1967: 220).

We found specimens similarly distorted in the following collections:

- Museum of Comparative Zoology: Alicetown, Bahamas; no. 13871;
- United States National Museum: Tortugas; no. 458-267;
- Academy of Natural Sciences, Philadelphia: St. Thomas; no. 55740 (2 specimens, "in madrepore").

The specimens in the Academy, interestingly enough found also in coral, measured:

height	width
45 mm	29 mm
54 mm	29 mm

These measurements indicate that the shells increased normally in height, but the increase in width was limited by the constriction imposed by the sides. Collectors have informed the senior author that such distorted *Lima* specimens are occasionally collected in other localities. The distortion of the valves thus results from this specialized habitat.

Gilmour (1967: 218) described the method by which *Lima hians* (Gmelin, 1791) widens the crevice in which its nest is to be built. "The animal usually started to burrow in a crevice between some of the larger fragments of the substratum. The crevice was enlarged by swimming backwards some distance, pausing, and swimming back into the crevice with considerable force. On the final propulsive stroke into the crevice the antero-ventral tentacles were quickly tucked between the shell valves and when the valves were pulled together the edges of the valves were driven into the crevice. The shell valves were then opened – so enlarging the crevice. By repetition of this cycle of movements the animal burrowed into the substratum." It may be assumed that the Mary Point *Lima* entered the *Lithophaga* burrow with considerably less effort and remained in its protected shelter until it was collected.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance of Dr. William K. Emerson of the American Museum of Natural History who read and checked the manuscript. The photographs were made by the junior author.

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Explanation of Figures *1* to *3*

Figure *1*: *Lima scabra* (Born, 1780) in *Lithophaga* burrow
Figure *2*: *Lima scabra*, normal shell
Figure *3*: *Lima scabra*, distorted shell

Figure *1*

Figure *2*

Figure *3*

Effect of Predation and Environmental Patchiness on the Body Size of a Tropical Pulmonate Limpet

BY

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(1 Plate; 3 Text figures)

INTRODUCTION

In recent years, a rapidly expanding body of knowledge on predation and its effects has focused attention on its importance in structuring communities (*e. g.*, Paine, 1966, 1969; Dayton, 1971; Hall, Cooper, & Werner, 1970). Particular emphasis has been placed on the impact of selective prey consumption, a trait previously recognized by zoologists as nearly universal among animals. A parameter of major significance in prey selection is prey size (Brooks & Dodson, 1965; Brooks, 1968; Dodson, 1970; Wells, 1970) and the work of Hall, Cooper, & Werner (*op. cit.*) suggests that the structure of many temperate pond communities largely revolves around size-selective predation and its effects. However, our knowledge of the functioning of tropical communities is relatively poor; hence, the generality of studies based on temperate communities is not entirely clear.

In this note I suggest that the dispersion and size frequency patterns of the tropical pulmonate limpet, *Siphonaria normalis* Gould, 1846 largely result from size-selective predation by a carnivorous gastropod, *Thais armigera* (Link, 1807).

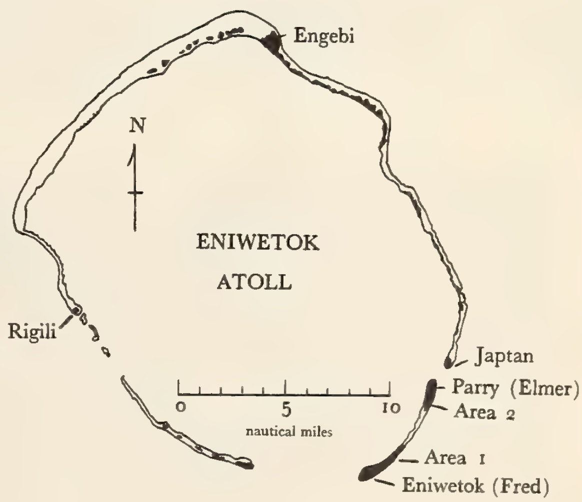

Figure 1

Map of Eniwetok Atoll, Marshall Islands. Areas 1 and 2 are the study areas on Eniwetok and Parry Islands, respectively. Prevailing winds are from the east-northeast. The black areas represent the islands, the outlined white areas represent the reef

STUDY AREAS

The study was carried out in August, 1970 on the seaward reef platforms of Eniwetok Island and Parry Island, two of about 40 islands on Eniwetok Atoll (latitude 11°21′ N, longitude 161°21′ E), Marshall Islands (Figure 1). The reef platform or bench is composed of a flat, homogeneous inner bench and an extremely heterogeneous fringing algal ridge (see Kohn, 1967; Tracey, Cloud, & Emery, 1955). Landward, the inner bench terminates abruptly against a steep beach of sand, shells and shell fragments of the gastropod genera *Conus, Drupa, Morula, Cerithium,* and *Cypraea* (Figure 2). The climate is tropical marine and prevailing conditions are warm temperate (daily maximum temperature is 30° C, minimum is 25.5° C), with high humidity, partly cloudy

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skies, moderate easterly tradewinds and occasional rain showers. The only notable seasonal change in weather is the usual occurrence of doldrums from June through October (U. S. Air Force, 1970).

Dominant macroinvertebrates on the reef include the gastropods *Thais armigera, Siphonaria normalis, Conus chaldeus* Röding, 1798, *C. ebraeus* Linnaeus, 1758, *Morula uva* (Röding, 1798), *Drupa morum* Röding, 1798, *Cypraea moneta* Linnaeus, 1758, *Cerithium* spp. and the hermit crabs *Calcinus* spp., *Diogenes* spp., and *Clibonarius* spp. In addition, individuals of the snails *Nerita plicata* Linnaeus, 1758 and *N. albiscillia* Linnaeus, 1758 occasionally wander onto the shoreward edge of the flat. Dominant type of algae on the inner bench were a non-calcareous red alga (?*Peyssonelia* sp.), a blue-green alga and encrusting melobesioid (coralline) algae; tufts of an unidentified filamentous brown alga and a red alga, *Martensia* sp., were locally abundant toward the seaward edge of the reef (personal observations; Dawson, 1956; assistance in identification from J. Norris).

There were three major differences observed between the two reef platforms. First, the Parry Island reef platform is slightly higher in elevation than the Eniwetok Island reef. Associated with this is the difference in types of algae present; on Parry Island virtually 100% of the substratum was covered with encrusting algae while on Eniwetok Island encrusting algae occurred in patches scattered in a "lawn" of algal "turf". Second, the gastropod *Thais armigera* is very rare at Eniwetok Island and locally abundant on Parry Island. Within the *Thais*-dense area (a 200 m stretch of shore) densities of 0.72/m² were recorded (a total of 316 m² were sampled); beyond the dense area, abundance of *Thais* was similar to that observed on Eniwetok Island, where a total of about 7 individuals were observed on a 2 km stretch of the reef. Although some *Thais* were certainly missed, it is clear that this gastropod was quite scarce (for unknown reasons) on Eniwetok Island. Third, the distribution of pulmonate limpets (size range: 1 to 12 mm), *Siphonaria normalis,* is characteristically patchy on Eniwetok Island, whereas on Parry Island they are distributed relatively evenly over the whole flat. The patchiness of *Siphonaria* on Eniwetok Island seems to result from the patchy distribution of a suitable substratum (*i. e.,* one covered only with encrusting algae, in this case coralline algae); in turn this may have resulted from the difference in elevation between the two reefs.

PATTERNS of DISTRIBUTION and ABUNDANCE of *Siphonaria normalis*

Mean densities of limpets within the *Siphonaria*-favorable patches on Eniwetok Island are somewhat higher than those on Parry Island (Table 1). Further, local differences in size-frequency exist at the latter area but not at the former. A comparison between the density and size of the limpets in the pools with encrusting coralline algae covering the bottom and those in pools with a very slippery *Peyssonelia*-like alga, reveals that coralline algae pools have many small *Siphonaria* and non-coralline pools contain a few large *Siphonaria.* Moreover, in proceeding from coralline algae pools to pool edges to emergent substratum between the pools ("ridges") on Parry Island, *Siphonaria* density decreases while mean individual size increases (Table 1, Figure *3*). This pattern does not occur on Eniwetok Island, where both density and limpet size are rather uniform within the *Siphonaria* patches (Table 1).

Observations of these limpets returning to home scars on Eniwetok Island (Figure *4*) confirms Cook's experiments (1969) on the homing behavior of this limpet. Local size or abundance patterns should therefore be affected little by migration. In the next section, I suggest that the primary cause of the patchy size-frequency distribution of *Siphonaria* is size-selective predation by *Thais* coupled with environmental heterogeneity.

Explanation of Figures *2* to *4*

Figure *2*: View of area 2 looking southwest towards Eniwetok Island (just visible in the center-left of the photograph). Note the shallow pools and the "ridges" between them. The cylindrical object in the right foreground is about 2 feet long and protects 20 to 30 *Thais armigera*

Figure *3*: Comparison between the size of *Siphonaria* in shallow tide pools (right) to that on the emergent substratum between the pools or "ridges" (left) at Parry Island (area 2). The dark color of the "ridge" substratum is caused by blue-green algae

Figure *4*: Close-up photograph of *Siphonaria in situ* and their "scars" or homing sites, several of which are vacant

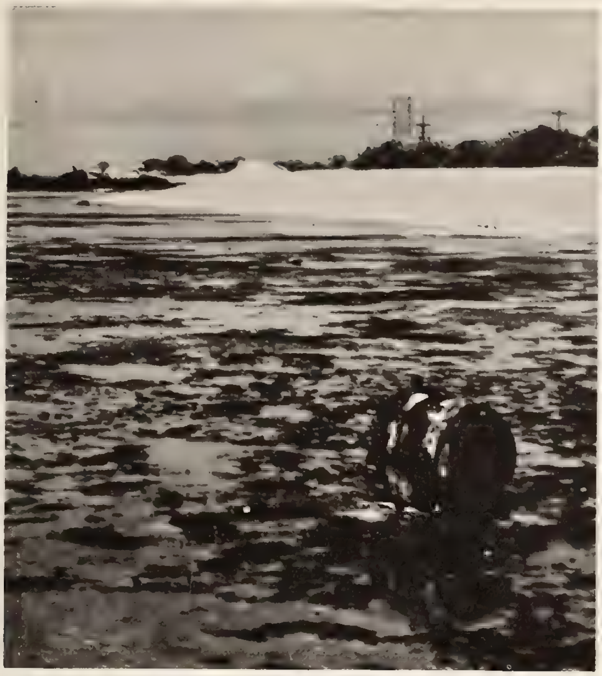

Figure 2

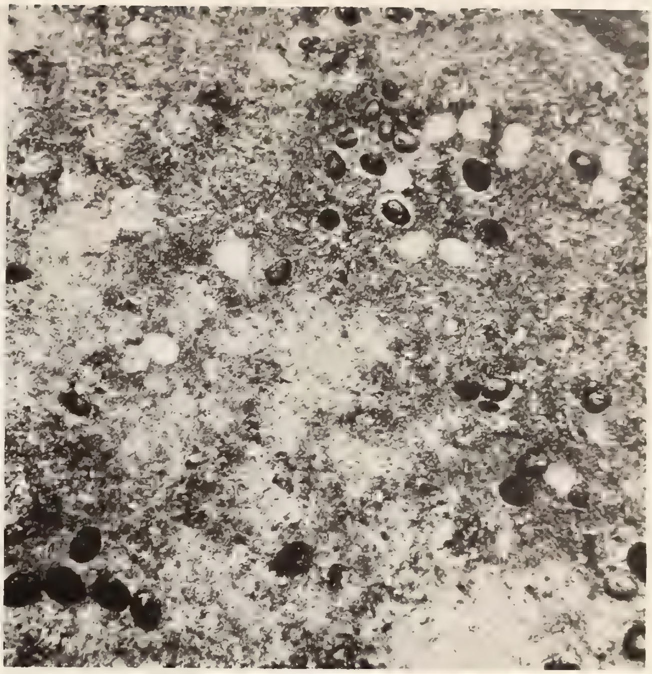

Figure 4

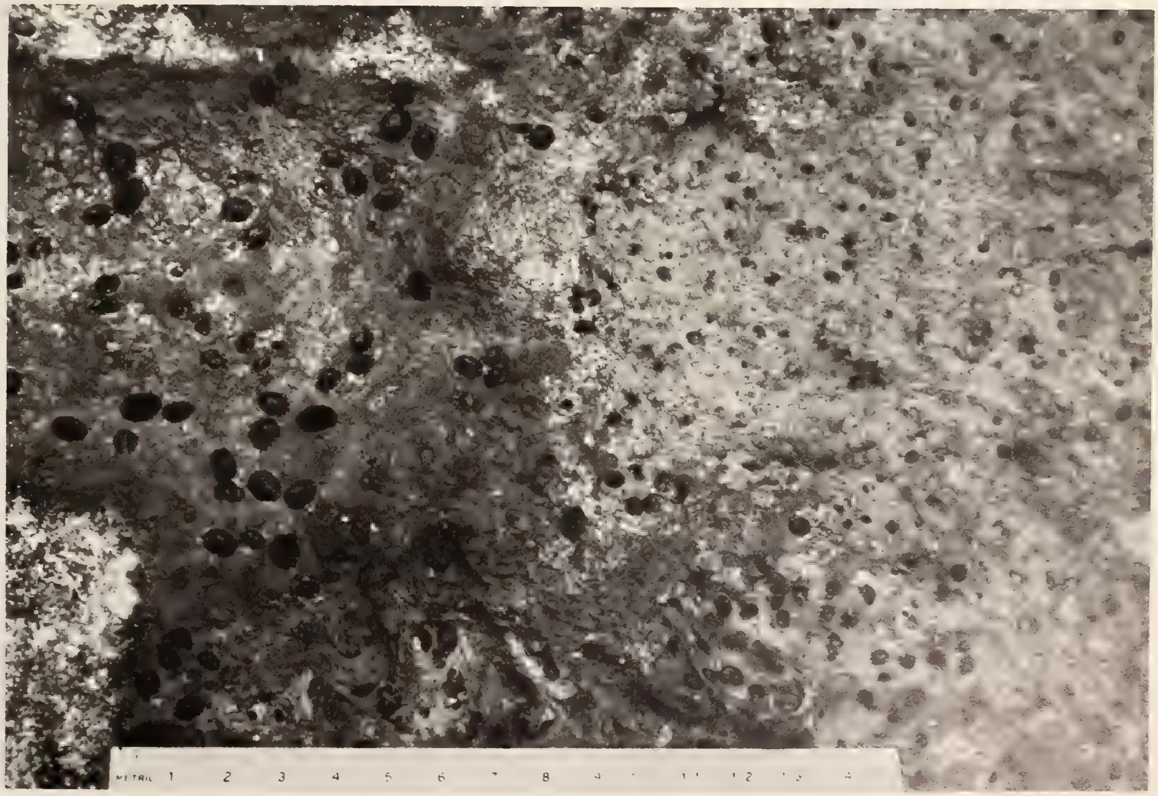

Figure 3

Table 1

Density of *Siphonaria normalis* at Two Areas on Eniwetok Atoll [2]

A. PARRY ISLAND

Substratum Characteristics	Density (no./m²) ±95% confidence interval	N	No. of quadrats where size of *Siphonaria* is predominantly [3] Large	Medium	Small
Encrusting non-calcareous algae, pool	150 ± 106	20	6	3	1
Encrusting coralline algae and detritus, pool	6150 ± 1329	19	0	5	12
Edge of pool	3361 ± 748	34	3	17	3
Dry substratum	438 ± 293	15	8	0	0
Average	2648 ± 620	81			

B. ENIWETOK ISLAND [4]

Substr. characteristics	Density (no./m²) ± 95% confidence interval	N
Encrusting coralline algae and detritus, damp	3473 ± 360	7

[2] Size of haphazardly placed quadrats: Parry Island, 100 cm²; Eniwetok Island, 400 cm²

[3] Totals do not equal N because some quadrats had no limpets in them

[4] Nearly all *Siphonaria* on Eniwetok Island were "medium" in size

FORAGING HABITS OF *Thais*

The majority of observations on *Thais armigera* were made on Parry Island. Capture of prey by *Thais* is accomplished by placing the head and anterior end of the foot over the relatively flat limpet and turning it over; once the limpet is positioned properly, *Thais* rasps the flesh out with its radula. (The mode of prey detection is unknown.) Feeding observations are made by turning over a *Thais,* examining it for prey, and measuring predator and prey length in millimeters.

Table 2 shows the percent of *Thais* feeding during a variety of tide and light conditions (excluding night high tides only). Feeding frequency was fairly constant during the interval of study, averaging 18.5% of the population over all tide and light combinations. The amount of variation in feeding and reproduction of *Thais* over longer intervals is unknown.

Table 2

Percent of *Thais armigera* Feeding at the Parry Island Study Area, August 1970

Date	Light and Tide	Number Observed	Number Feeding	% Feeding
8/VIII/70	Day Low Tide	104	21	20.2
13/VIII/70	Day High Tide	234	32	13.7
14/VIII/70	Day High Tide	91	18	19.8
18/VIII/70	Night Low Tide	150	27	18.0
23/VIII/70	Day Low Tide	130	27	20.8
Total		709	125	18.5

In August, 1970, the diet of *Thais* was nearly monospecific, with the *Siphonaria* accounting for 99.2% (131) of the observations and the herbivorous snail, *Nerita albiscillia,* accounting for the remaining 0.8% (1 individual). Other molluscan prey are rare in the environment, but might be eaten by *Thais* if encountered.

DISPERSION PATTERN OF *Thais*

The dispersion pattern of *Thais* and the percent of the population feeding suggest that relatively more of its time is spent feeding in tide pools. The direction of deviation of the observed distribution of *Thais* from a Poisson (random) pattern of distribution indicates that at low tide this snail is contagiously distributed on the reef flat (*i.e.,* there are more 1 m² quadrats with 3 and 4 *Thais* per quadrat and fewer with 1 and 2 than expected by chance alone; see Figure 5). Although the cause of this contagion is not known, two observations suggest that desiccation plays a major role in patterns of *Thais* dispersion. First, *Thais* microdistribution is strongly correlated with that of the small, shallow pools scattered over the reef (Table 3) at low tide; 83.2% of 113 *Thais* were observed in these pools, with a total of 92.1% observed on "wet" substratum. Subjective estimates of the percent of the substratum covered by tide pools (in 80 1-m² quadrats) indicate that 65.4±4.0% of the total Parry Island area is underwater at low tide. Thus *Thais* appears to be in tide pools more

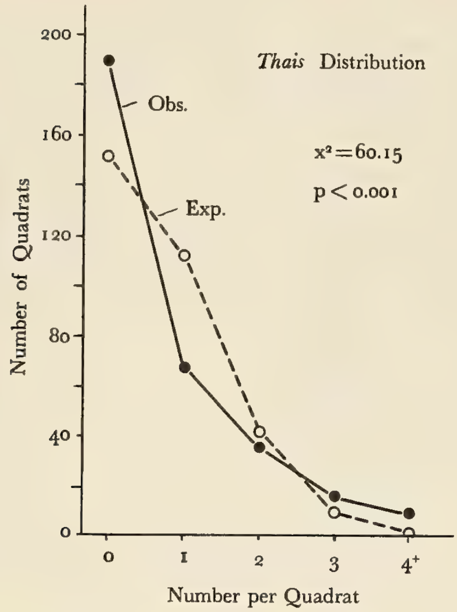

Figure 5

Comparison between the observed number of quadrats containing 0, 1, 2, 3, and 4 or more *Thais* and the number expected. Chi square shows that the observed curve is significantly different from the expected (Poisson) distribution (*i. e.*, the *Thais* are non-randomly distributed)

Table 3

Thais armigera Distribution According to Wetness of Substratum

Substratum type	Number of *Thais*	% of total
Wet - Tide pools	94	83.2
- Depressions	8	7.1
- "Ridges"	2	1.8
Wet Total	104	92.1
Dry - Depressions	6	5.3
- "Ridges"	2	1.8
- Top of Rock	1	0.9
Dry Total	9	8.0
Grand Total	113	100.1

frequently than expected by chance, suggesting that there is a preference for wet habitats. Second, observations of the distribution of *Thais* under and around a cylindrical piece of scrap metal located within the *Thais* patch on Parry Island (shown in Figure 2) show that about 20 - 30 *Thais* are located around and under the metal object. A zone of about 6m radius around this object contained virtually no *Thais,* and beyond this zone densities increased to the normal 0.7/m². Since *Siphonaria* are distributed over both wet and dry substratum (Table 1) and pools afford no obvious shelter to *Thais* from potential predators, the most probable factor responsible for this apparent preference for wetness or cool, damp crevices is desiccation or some related physical factor. This preference for tidepools at low tide means that a relatively greater proportion of this predator's time budget will be spent in such microhabitats. Hence, the *Siphonaria* in pools would probably be subject to more intense predation than those outside the tidepools.

In view of these data, several hypotheses can be proposed to explain the observed size-frequency pattern of *Siphonaria* (Figure 4, Table 1). First, size-selective predation by *Thais* (which spends relatively more of its time in pools) may cause the observed pattern. Second, *Siphonaria* may settle preferentially in the pools and gradually migrate to the ridges. Third, *Siphonaria* may settle uniformly over the reef flat, but perhaps because of desiccation, survive better in the pools than on the ridges. In this case, the few survivors on the ridges would have more food available (assuming little difference in availability of food for the limpets existed between pools and ridges) and would grow large because of their reduced density. Fourth, considering that in certain tidepools (*i.e.*, those with ?*Peyssonelia* as the dominant encrusting algae; Table 1) limpet density and size pattern were similar to those on the ridges, a cause of the patterns observed may reside in some subtle effect of the substratum or food on *Siphonaria.* Finally, a hypothesis combining elements of the above three hypotheses is that *Thais* may crawl to the ridges for food and return to the pools to consume any prey captured.

The data in Figure 6, which compare the size frequencies of *Siphonaria* available in the pools and on the "ridges" to the size of limpets eaten by *Thais,* support the first hypothesis by showing that this snail selects the largest prey available. The observation that the *Siphonaria* size pattern noted above does not occur on Eniwetok Island, where *Thais* is virtually absent provides further support for this hypothesis. Because nothing was known about *Siphonaria* reproduction and time was limiting, it was not possible to test the other hypotheses. However, the homing response of *Siphonaria* (Cook, 1969; see above) mitigates against the second hypothesis and, since in most cases, *Thais* were observed to consume prey on or near the site of capture, the last hypothesis is viewed as unlikely as

well. The third and fourth hypotheses remain reasonable possibilities.

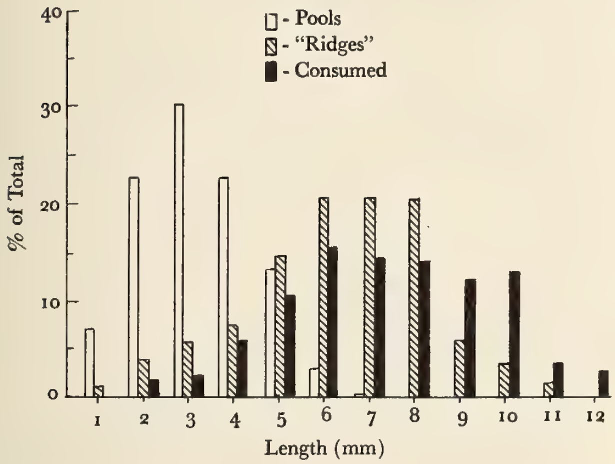

Figure 6

Size frequency histogram comparing the sizes of *Siphonaria* in pools and on "ridges" to the size eaten by *Thais armigera*

DISCUSSION

Although limited in their temporal extent, the data presented above provide a compelling argument that the absence of large *Siphonaria* from tidepools is largely caused by size-selective predation by *Thais armigera*. As yet unanswered are the effects of desiccation, food preference, and palatability on this size-frequency pattern.

Despite the fact that ecologists have long been aware of the importance of increasing our knowledge of tropical ecosystems, particularly with respect to understanding the causes of patterns of species diversity, we remain essentially ignorant of the relative effects of predation and competition in the tropics. I believe that unequivocal statements regarding the causes of patterns of distribution, size, abundance, and thus the causes of differences in species diversity, will ultimately be obtained by the proven and powerful manipulative-natural historical type of research (*e.g.*, CONNELL, 1961a, 1961b, 1970; PAINE, 1966, 1969, 1971; DAYTON, 1971; HALL, COOPER, & WERNER, 1970; MENGE, 1972). Although the major value of this report is clearly heuristic, I feel this paper represents a small step toward the clarification of the role of invertebrate predators in the tropics.

ACKNOWLEDGMENTS

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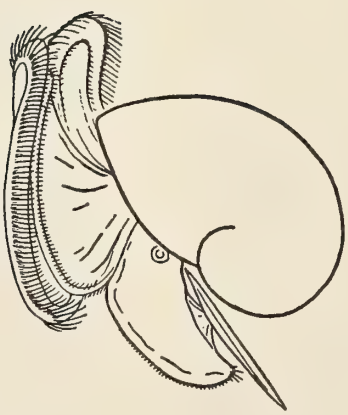

Maintaining Adult Bivalves for long Periods on Artificially Grown Phytoplankton

BY

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KEEPING BIVALVES ALIVE in a laboratory by addition of artificially cultivated phytoplankton to sea water is not new and was practiced at U. S. Fisheries Laboratory at Milford, Connecticut, for a number of years (LOOSANOFF & ENGLE, 1947; LOOSANOFF & DAVIS, 1963). In those cases, however, the water passing through the laboratory contained natural plankton and, of more importance, maintenance of animals under such conditions was of relatively short duration, rarely exceeding 2 or 3 months. Because of the circumstances described herein this report discusses observations made under rather radically different conditions.

In October of 1971 two groups of mussels, *Perna canaliculus* (Gmelin, 1791), were shipped from New Zealand to the Pacific Marine Station located near the entrance to Tomales Bay on the central coast of California. One of the groups was collected near Auckland, North Island, and the other was shipped from Marlborough Sound, South Island. The mussels were imported for studies of their physiological and ecological requirements. They were introduced into California with the knowledge of the New Zealand fishery authorities and permission of the State of California Department of Fish and Game.

Upon arrival the mussels were placed in running sea water which, after passing through water tables containing the mollusks, is discharged into a special dry well located more than 1800 feet (540m) from the seashore. Thus, to avoid the introduction of undesirable exotic organisms into California waters the mussels have been kept in strict quarantine.

As is well known, mussels are filter-feeding animals, existing principally on marine phytoplankton. However, the peculiarity of the sea water system at the Pacific Marine Station is such that before entering the storage tanks it is drawn through a layer of sand and therefore becomes virtually devoid of natural plankton. Since the mussels would starve under such conditions, a method had to be employed for introducing relatively large quantities of phytoplankton into the water. The problem was solved on the basis of our previous experience in growing phytoplankton on a massive scale by enriching stored sea water with commercial fertilizers (LOOSANOFF & ENGLE, 1942; LOOSANOFF, 1951). Briefly, in the present experiment we use 2 redwood tanks, 8 feet (2.4 m) in diameter, and approximately 24 inches (60 cm) deep, which are filled with sea water to a depth of about 18 inches (45 cm), and then enriched with tobacco fertilizers designated by the formula 6 - 3 - 6 at the rate of 0.5 gr per liter. This fertilizer is used by tobacco growers in Connecticut. Other fertilizers containing no insecticides and weedicides were also quite efficient. The tanks are aerated continuously to maintain the plankton in suspension and to expose the individual cells to the effect of light. During winter the cultures are illuminated and warmed by incandescent lamps kept burning continuously over the tanks.

The mass cultures were inoculated with several species of algae, but *Phaeodactylum tricornutum* (Bohlin) was normally predominant, although *Dunaliella tertiolecta* (Butcher) was also of common occurrence, though in much smaller numbers. The cultures were started about 2 weeks apart to prevent their becoming too old, because it was found in the past that such cultures may be toxic to bivalves (LOOSANOFF & ENGLE, 1947; LOOSANOFF & DAVIS, 1963). Usually the cultures became quite dense within a week after the inoculation, the color being light brown because of the preponderance of *P. tricornutum*.

The plankton culture was fed into the troughs containing the mussels and mixed at the entrance with the running sea water. The mussels readily digested the plankton

cells and formed normal feces. In cases when too much food was introduced, excessive quantities of pseudofeces were formed, but as soon as the situation was corrected normal feeding behavior resumed.

Except for several cases of initial mortality caused by the stress experienced during shipment, the mussels suffered virtually no losses for a period of about 9 months. During this time many individuals in both groups showed new shell growth, and natural, apparently normal, spawning occurred on at least two occasions. Towards the end of the year, however, several large mussels of the northern group died, but at the time this report is being written the majority of the mussels of the southern group and approximately 75% of the northern mussels are still living after being artificially fed for more than 17 months.

We are not aware of the exact cause of the mortality of the mussels, but it is possible that since our plankton cultures consisted, as a rule, of only one or two species of diatoms, the diet may have been deficient in some respects. This situation is easily correctable by growing more diversified mass cultures. Another probable cause of the mortality was stress due to several failures in the sea water system at which time the mussels received only recirculated sea water. In one instance when the mussels were kept under this condition for 8 days, mortality sharply increased.

Thus, even with limited facilities, it has been demonstrated that bivalves may be successfully kept alive for a period of about a year and a half while being fed exclusively artificially grown phytoplankton. These observations clearly illustrate once more the possibility for maintaining and raising, possibly far from the ocean, such mollusks as mussels, oysters, and clams, as well as other filter-feeding organisms, for at least 17 months in sea water lacking natural food. They also suggest many practical uses in mariculture, especially in shellfish farming.

ACKNOWLEDGMENT

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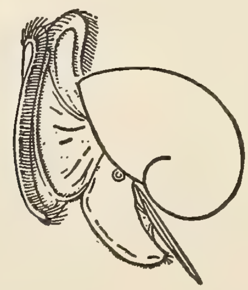

Trace Metal Levels in Three Subtidal Invertebrates

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(2 Text figures; 1 Map)

INTRODUCTION

The determination of metal concentrations in marine organisms is becoming increasingly necessary for ecological study due to interactions of essential trace metals with toxic heavy metals. The significance of trace metals in the marine biosphere was documented many years ago (Cornec, 1919; Clarke & Wheeler, 1922), and research in this field has flourished with the improvement of analytical methods. Reviews by Vinogradov (1953) and Goldberg (1967) demonstrate increasing importance of heavy metals in the marine environment.

The accelerated research in heavy metal analysis has led to greater knowledge of the elemental levels in several marine organisms (Brooks & Rumsby, 1965; Culkin & Riley, 1958; Bertine & Goldberg, 1971; Graham, 1972). However, the marine environment being extremely complex, diverse, and in constant flux, comparatively few organisms have been analyzed for their elemental content.

The objectives of this study were: 1) to determine the levels of aluminum, barium, cadmium, calcium, copper, iron, lead, magnesium, manganese, nickel, potassium, silver, sodium, strontium, and zinc in the herbivorous gastropod *Olivella biplicata* (Sowerby, 1825), the predatory gastropod *Polinices lewisii* (Gould, 1847) and the predatory sea star *Pisaster brevispinus* (Stimpson, 1857) (these latter two species prey upon *Olivella* – see Edwards, 1969); 2) to clarify the relationship of metals between the two trophic levels; 3) to define the range and variability of

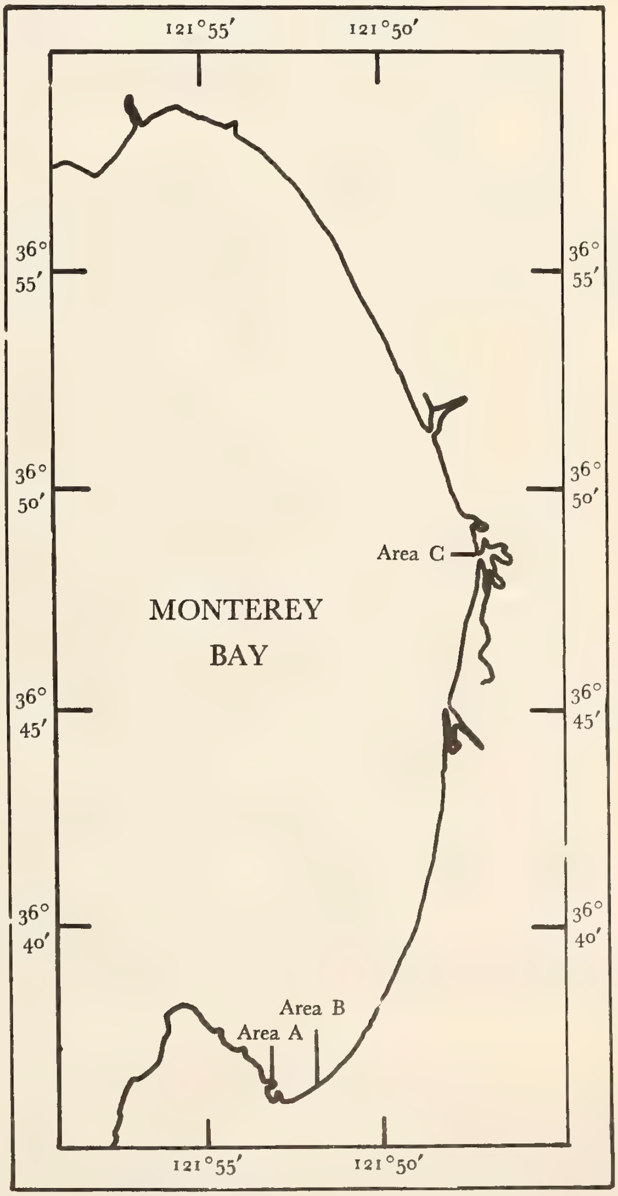


Figure 1

(adjacent column →)

Sampling Sites around Monterey Bay, California
Area A: Fisherman's Wharf, Monterey; Area B: Monterey Sewage Outfall, Monterey; Area C: Elkhorn Slough, Moss Landing

metal concentrations within the same species with respect to geographic location, and 4) to determine the difference in elemental concentrations between certain tissues.

METHODS

Olivella, Polinices and *Pisaster* were collected subtidally on sandy beaches (Figure 1) and placed in plastic bags. In the laboratory, the animals were placed in filtered sea water in aquaria and allowed to purge themselves of sediments for a minimum of 24 hours. The gastropods were boiled in distilled water for 3 to 5 minutes. This allowed the soft parts to be easily separated from the shells with a plastic fork or stainless steel forceps. Both the shell and soft tissue were oven dried at 65° C for a minimum of 48 hours.

The sea stars were dissected with stainless steel scissors immediately after purging in sea water. Part of one ray (not including hepatic caecum or gonads), hepatic caecum, gonadal tissue, and a combination of the pyloric stomach, cardiac stomach and rectal caeca were dissected, placed in tared beakers, and oven dried.

When dry, the soft parts were ground to a fine powder with mortar and pestle. The *Pisaster* ray homogenate contained particles of about 5 mm across or smaller. The gastropod shells were not ground. The *Polinices* shells were separated into 4 parts: operculum, anterior, posterior, and spire. The *Olivella* shells were digested whole.

Aliquots were weighed into tared beakers and digested with 70% or 90% nitric acid. Shells were digested with concentrated hydrochloric acid. The samples were left at room temperature for one hour, refluxed for one hour, and evaporated to 5 ml. Two to three milliliters of 30% hydrogen peroxide added dropwise oxidized any remaining organic matter. One ml of hydrochloric acid was added and the samples were adjusted to a final dilution (1%) with distilled water.

The samples were analyzed by atomic absorption. Reagent blanks were run with each group of samples. Readings of less than 2% absorption were discarded due to probable background effects.

Means and 95% confidence intervals were determined using the expression $t\sqrt{x/N}$, where $\sqrt{x/N}$ is the standard error of the mean for $N < 30$, and t is the Student's t value for N–1 degrees of freedom (Elliott, 1971).

RESULTS and DISCUSSION

Means and 95% confidence intervals of the metal concentrations in the *Olivella, Polinices,* and *Pisaster* soft and hard parts are listed in Table 1. Concentrations of aluminum, cadmium, copper, iron, lead, manganese, nickel, silver, and zinc for *Olivella* and *Polinices* soft parts, and selected *Pisaster* tissues from different localities are presented in Figure 2 and Figure 3, respectively. The results are discussed individually for each element with respect to geographical location, trophic level, and physiological parts. Barium, calcium, magnesium, potassium, sodium, and strontium values are not discussed but are listed in Table 1. All elemental values are expressed as μg/g (ppm) and ppm is used throughout the text.

Aluminum: *Polinices* had highest levels at Fisherman's Wharf (50.6 ± 7.5 ppm) and *Olivella* had highest values at Elkhorn Slough (98.5 ± 12.3 ppm) and lowest at Monterey Outfall (59.6 ± 19.2 ppm). These values are similar to the 50 ppm level described by Vinogradov (1953). The high values of *Olivella* at Elkhorn Slough are probably due to the greater amount of clay particles in suspension in this area.

Cadmium: Mullin & Riley (1956) found cadmium levels in Mollusca of 3 ppm, and levels in Echinodermata of 1 ppm. These levels are consistent with those in this study for *Olivella* (2.3 ± 1.9 ppm to 4.2 ± 5.1 ppm) and *Polinices* (0.3 ± 0.5 ppm to 1.6 ± 1.3 ppm). Graham (1972) found cadmium levels in the gastropod *Tegula funebralis* (A. Adams, 1855) at Fisherman's Wharf of 2.2 ppm. *Pisaster* hepatic caecum was found to have high Cd levels (46.3 ± 20.6 ppm) at the Monterey Outfall.

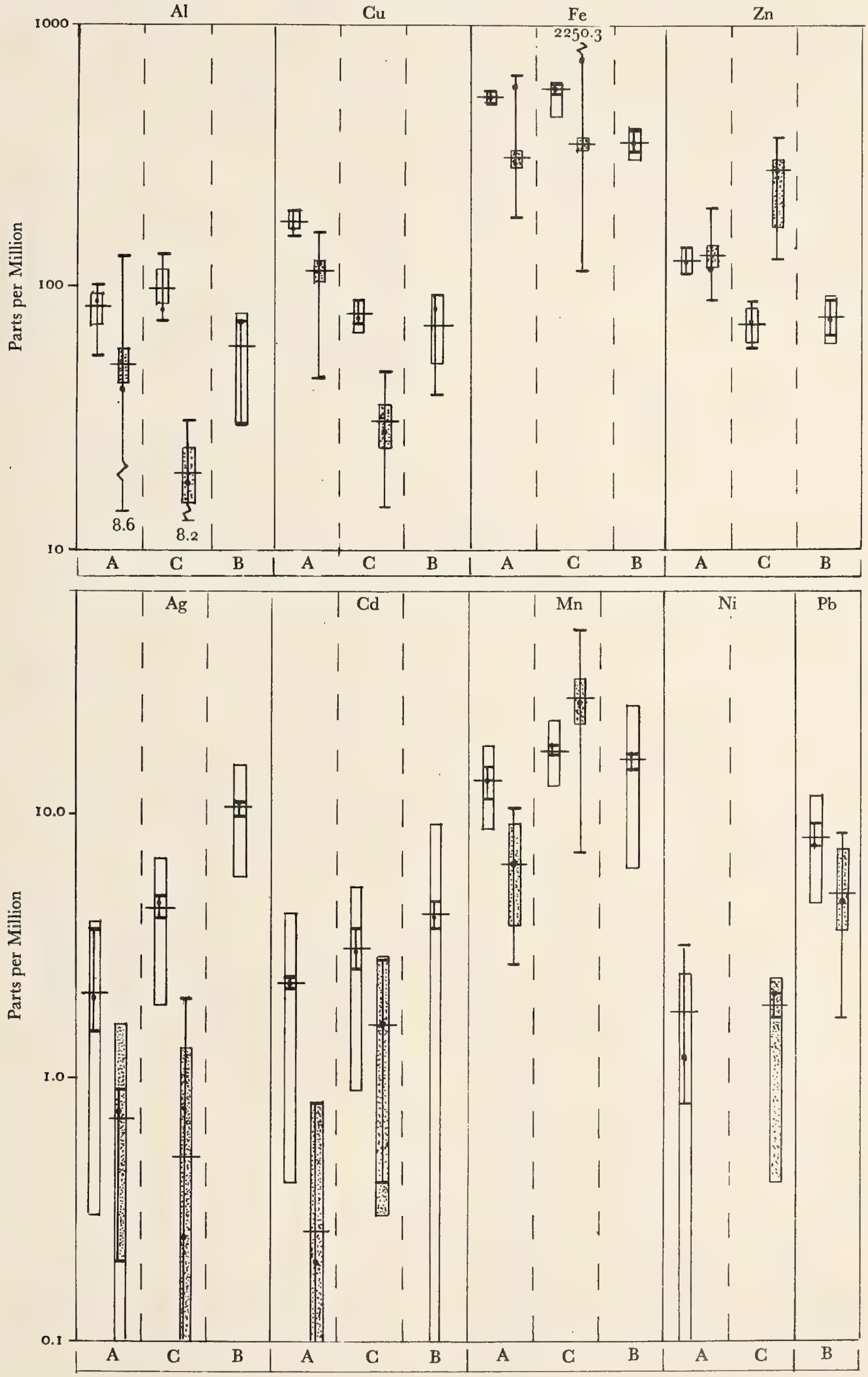
Cadmium is a known contaminant of the biosphere (Nilsson, 1970). Cadmium and zinc occur synergistically in nature. Besides being a general cytotoxic agent, cadmium competes with zinc and copper for the same binding sites.

Copper: Levels of 4 ppm to 50 ppm (Vinogradov, 1953) are much higher than copper levels in sea water, 3×10^{-3} μg/l (Goldberg, 1963), yet much lower than copper levels observed in experimental animals. Fisherman's Wharf had the highest values of copper: *Olivella* – 177.3 ± 16.5 ppm; *Polinices* – 115.4 ± 11.3 ppm. Graham (1972) and Fitz (1971) found copper concentrations at Fisherman's Wharf in *Tegula funebralis* and *Emerita analoga* (Stimpson, 1857) to be 175 ± 9.0 ppm and 71 to 90

Figure 2

(on facing page →)

Comparison of *Olivella biplicata* (clear) and *Polinices lewisii* (stipple) soft parts: Means, Medians, Range, and 95% confidence Intervals (see Figure 3 for symbol explanation)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Cu
Fe
Zn
2250.3
1000
100
10
Parts per Million
8.6
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A
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Cd
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10.0
1.0
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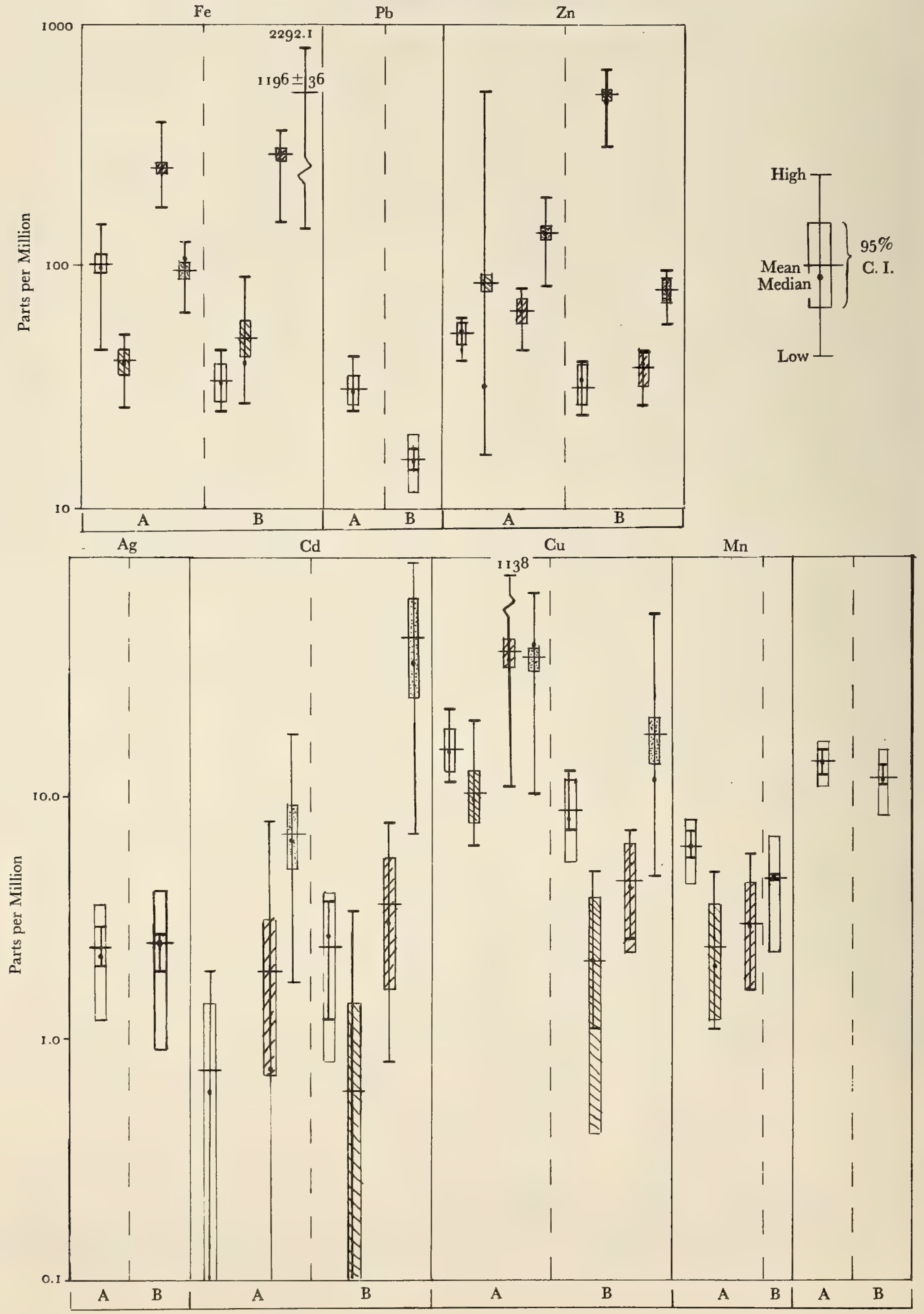
Fe
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Parts per Million
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High
Mean
Median
Low
95%
C. I.
Ag
Cd
Cu
Mn
1138
10.0
1.0
0.1
Parts per Million
A
B
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A
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B

ppm, respectively. *Pisaster* had higher copper levels at Fisherman's Wharf than at the Monterey Sewage Outfall. It is not known why these levels are highest at the Wharf. Perhaps high copper values are related to pollution from boats.

Copper, a highly electronegative metal, is classified as a metallo-enzyme (BOWEN, 1966). This high electronegative quality may act to destroy or deactivate enzymes. ADELSTEIN & VALLEE (1962) and UNDERWOOD (1971) cited that haemocyanin, an important copper-containing respiratory pigment in various gastropods and other marine species, was a constituent in blood plasma. On this basis one would expect to find this element concentrated in gastropod soft parts.

Iron: *Olivella* had the lowest iron levels (358±47 ppm) at the Monterey Sewage Outfall, while *Polinices* levels remained equal at both localities. These values, although lowest, are still above the 200 ppm level for Mollusca and 300 ppm level for Echinodermata reported by VINOGRADOV (1953). CULKIN & RILEY (1958) show that *Littorina littorea* (Linnaeus, 1758) and *L. littoralis* (Linnaeus, 1758), gastropods from the Irish Sea, have values within Vinogradov's limits, 171 ppm and 229 ppm, respectively.

Gastropod shells were found to be highest in iron at the Fisherman's Wharf site. *Olivella* shells had mean values of 74.6±6.2 ppm, while anterior parts of the *Polinices* shell had a value of 81.1±22.4 ppm. *Pisaster* data suggested that the soft parts were concentrating more iron at the Outfall, while the ray was higher at Fisherman's Wharf. Iron is found in high concentrations in clay, and so the high values may be natural levels. The high value at Fisherman's Wharf could, however, be attributed to the iron structures located there.

Iron, like many other elements, is essential for life. As an enzyme-activating metal, iron is able to activate many oxidases involving molecular oxygen. However, iron is more commonly considered a metallo-enzyme, because it is more firmly bound to a protein in constant stoichiometric ratios rather than loosely held. One such metalloprotein, echinochrome, is found in echinoderm blood (CANNAN, 1927).

Figure 3

(← on facing page)

Comparison of *Pisaster brevispinus* tissues:
Ray (clear), Gonad (positive diagonal slope), Stomach (negative diagonal slope), and Hepatic Caecum (stipple). Means, Medians, Range, and 95% confidence Intervals (see legend for symbol explanation)

Lead: Levels of lead were found to be greatest for *Olivella* at Fisherman's Wharf (8.2±3.6 ppm) and *Polinices* (5.0±2.4 ppm) soft parts. GRAHAM (1972) found the gastropod *Thais emarginata* (Deshayes, 1839) to have levels of 9.8±4.0 ppm in lead at Fisherman's Wharf. *Olivella* shells were lowest at the Wharf, with highest values at Elkhorn Slough. *Polinices* shells also had highest concentrations at Elkhorn Slough. *Pisaster* tended to concentrate lead in the rays, with higher lead values in *Pisaster* at Fisherman's Wharf than at the Monterey Outfall (30.9 ±4.3 ppm and 15.9±4.2 ppm, respectively). These high values for the shells and *Pisaster* rays may be due to scattering of light.

BOWEN (1966) classified lead as a very high potential pollutant. Lead occurs chiefly as a contaminant, and can produce toxic effects by combining with cellular membranes to alter permeability (PASSOW, 1969). Cadmium and copper may also produce toxic effects by acting on membrane permeability (PASSOW, *op. cit.*) Lead contamination is very high (0.07 to 0.35 μg Pb/kg sea water) in the marine environment (PATTERSON 1971). Soil contains 10 ppm (BOWEN, *op. cit.*), and stated levels for mollusks and echinoderms are 0.7 ppm and 187 ppm, respectively (VINOGRADOV, 1953).

Manganese: Manganese has been reported at 60 ppm in Echinodermata and 10 ppm in Mollusca (VINOGRADOV, 1953). *Polinices* was found to have the highest concentration of Mn at Elkhorn Slough (27.5±5.5 ppm), while levels in *Olivella* soft parts remained consistent, as did levels in rays of *Pisaster*. Manganese levels in *Pisaster* soft parts were very low (non-detectable to 3.0±1.4 ppm).

Manganese is another element that is essential for life. It is considered an enzyme-activating metal (VALLEE, 1955), and was found to activate certain phosphate transferases and decarboxylases (BOWEN, 1966). Organically bound Mn is found in Mollusca (VINOGRADOV, *op. cit.*), one of these proteins being pinnaglobin (BOERI, 1963).

Nickel: *Olivella* bodies had highest concentrations at Fisherman's Wharf (1.8±1.7 ppm), and *Polinices* was highest (1.9±1.5 ppm) at Elkhorn Slough. These values compare with 4 ppm for Mollusca (VINOGRADOV, 1953). *Olivella* shells were much higher than the soft parts (16.9±2.9 ppm), and the same is true for *Polinices* shells (16.2±8.4 ppm). *Pisaster* rays were found to have higher concentrations than other tissues; however, these high values may be due to scattering of light caused by the large amounts of calcium in the samples. Nickel affects several enzymes *in vitro* – activation of arginase, carboxylase, trypsin, citritase, and inhibition of acid phosphatase – but is not necessary for proper functioning.

Silver: Vinogradov (1953) reported molluscan levels as 0 ppm and echinoderm levels as 3? ppm. Since sea water contains only $3 \times 10^{-4} \mu g/l$ (Goldberg, 1963), these relatively low levels are quite high enrichment factors. *Olivella* bodies were found to be much higher at Monterey Outfall than at any other area (10.7 ± 4.8 ppm). The rays of *Pisaster* contained equal concentrations and were higher than other tissues. This high value in the rays may be due to scatter. Veith (1971) reported effluent levels of many metals from the Monterey Sewage Outfall, silver having a concentration of 25 ppm in the effluent. This high input directly into the biosphere could possibly explain the high *Olivella* values.

Silver, an electronegative metal, has a strong affinity for imino, amino, and sulphydryl groups (Bowen, 1966). These groups are most likely reactive sites on many enzymes, and hence silver has the capacity to deactivate the enzyme. It follows that silver therefore is a poison, by virtue of its reactivity with proteins, especially enzymes. Silver competes with copper, but probably does not inhibit the copper enzyme (Christian & Feldman, 1970).

Zinc: *Polinices* soft parts had highest concentrations at Elkhorn Slough (288 ± 18 ppm) and *Olivella* bodies were highest at Fisherman's Wharf (127 ± 14 ppm). Graham (1972) found zinc levels in *Tegula funebralis* to be 198 ± 7 ppm. These values all correspond with those in Vinogradov (1953) of 200 ppm for mollusks and 25 ppm for

Table 1

Mean and 95% Confidence Intervals in Parts per Million

	Date obtained	Part of Animal	Area [1]	N [2]	Silver	Aluminum	Barium	Calcium
1.	19/IV/72	*Olivella*: soft	A	32	2.1 ± 1.8	83.9 ± 11.4	—	2463 ± 62
2.	13/ V/72	*Olivella*: soft	C	32	4.4 ± 2.5	98.5 ± 12.3	—	2312 ± 59.7
3.	14/ V/72	*Olivella*: soft	B	13	10.7 ± 4.8	59.6 ± 19.2	—	600.6 ± 60.9
4.	19/IV/72	*Olivella*: shell	A	10	4.2 ± 1.5	—	—	458830 ± 485
5.	13/ V/72	*Olivella*: shell	C	6	3.4 ± 1.9	—	—	545948 ± 776
6.	14/ V/72	*Olivella*: shell	B	6	3.5 ± 2.0	—	—	633076 ± 988
7.	19/IV/72	*Polinices*: soft	A	6	0.7 ± 0.9	50.6 ± 7.5	—	718.6 ± 28.1
8.	13/ V/72	*Polinices*: soft	C	6	0.5 ± 0.8	19.8 ± 4.7	—	732.7 ± 28.4
9.	19/IV/72	*Polinices* operculum	A	3-5	0.4 ± 0.2	—	—	733.0 ± 43.3
10.	13/ V/72	*Polinices* operculum	C	6	—	172.5 ± 12.0	—	384.2 ± 20.6
11.	19/IV/72	*Polinices* shell-anterior	A	3-5	2.0 ± 3.0	—	—	398821 ± 1569
12.	13/ V/72	*Polinices* shell-anterior	C	4	3.2 ± 2.8	—	—	449335 ± 10670
13.	19/IV/72	*Polinices* shell-spire	A	3-5	2.5 ± 3.5	—	—	415198 ± 1601
14.	13/ V/72	*Polinices* shell-spire	C	4	4.6 ± 3.4	—	—	308044 ± 8830
15.	19/IV/72	*Polinices* shell-posterior	A	3-5	2.0 ± 3.5	—	—	458204 ± 1682
16.	13/ V/72	*Polinices* shell-posterior	C	4	3.8 ± 3.1	—	—	492895 ± 11170
17.	19/IV/72	*Pisaster* ray	A	9	2.4 ± 1.2	—	—	62827 ± 193
18.	9/ V/72	*Pisaster* ray	B	6	2.5 ± 1.6	—	—	106132 ± 3419
19.	19/IV/72	*Pisaster* gonad	A	9	—	—	—	668.7 ± 19.9
20.	9/ V/72	*Pisaster* gonad	B	5	—	—	—	1527 ± 48.5
21.	19/IV/72	*Pisaster* stomach	A	8	—	—	—	1014 ± 26.6
22.	9/ V/72	*Pisaster* stomach	B	6	—	—	—	1580 ± 41.7
23.	19/IV/72	*Pisaster* hepatic caecum	A	9	—	—	—	118.6 ± 10.6
24.	9/ V/72	*Pisaster* hepatic caecum	B	6	—	—	—	1153 ± 42.2

[1] Area 1: Fisherman's Wharf, Monterey
Area 2: Monterey Sewage Outfall
Area 3: Elkhorn Slough

[2] N = Number of animals

— non-detectable value

echinoderms. *Pisaster* displays an interesting pattern as to zinc concentration. The Wharf site was higher in all tissues except for the gonads. At the Outfall, the gonads were excessively high, with values averaging 511.9±28.1 ppm. Echinoderm gonads are known to contain high zinc levels (*in litt.*, Martin). Those *Pisaster* collected at the Outfall had less developed gonads than those from Fisherman's Wharf. This may be the reason why specimens from these two localities differed in zinc concentrations. Another possibility could be the high zinc effluent from the Monterey Outfall of 820 ppm (Veith, 1971).

Zinc, a metallo-enzyme, is essential to most life forms (Bowen, 1966). Zinc can displace copper from a protein, and hence act as an antagonist, or can compete in some proteins with cadmium for binding sites.

Trophic Magnification: Much attention has been given to the problems of biological magnification of DDT, DDE, PCBs (polychlorinated biphenyls), and other halogenated hydrocarbon concentrations (Woodwell, 1967; Johnson *et al.*, 1971; Nimmo *et al.*, 1971). Upon analysis of Table 1, it seems evident that heavy metals do not concentrate through the trophic levels of the organisms studied.

SUMMARY

Although concentrations of heavy and trace metals are not magnified through the studied trophic levels, this

Table 1 [continued]

Mean and 95% Confidence Intervals in Parts per Million

Cadmium	Copper	Iron	Potassium	Magnesium	Manganese	Sodium	Nickel	Lead	Strontium	Zinc
2.3 ± 1.9	177.3 ± 16.5	530.3 ± 28.6	8682 ± 116	9798 ± 123	13.5 ± 4.6	915.0 ± 37.6	1.8 ± 1.7	8.2 ± 3.6	56.3 ± 9.3	127 ± 14
3.1 ± 2.2	78.9 ± 11.0	573.8 ± 29.7	12438 ± 1385	6542 ± 100	17.7 ± 5.2	18222 ± 1676	—	—	48.3 ± 8.6	72.5 ± 10.6
4.2 ± 5.1	71.5 ± 21.0	357.6 ± 47.0	16749 ± 3215	5650 ± 187	16.3 ± 10.0	15604 ± 3103	—	—	25.9 ± 12.6	77.2 ± 16.1
—	—	74.6 ± 6.2	59.9 ± 5.5	—	—	2903 ± 38.5	16.9 ± 2.9	—	1092 ± 23.6	—
0.2 ± 0.4	4.4 ± 2.2	20.4 ± 4.7	62.4 ± 8.3	84.0 ± 9.6	7.4 ± 2.9	6800 ± 102	17.5 ± 4.4	22.6 ± 5.0	527.9 ± 24.2	1.9 ± 1.5
—	3.4 ± 1.9	16.0 ± 4.2	47.5 ± 7.2	75.4 ± 9.1	3.9 ± 2.1	10659 ± 108	15.2 ± 4.1	20.7 ± 4.8	100.7 ± 10.5	2.2 ± 1.6
0.3 ± 0.5	115.4 ± 11.3	312.6 ± 18.6	2066 ± 47.7	3463 ± 62	6.5 ± 2.7	10880 ± 110	—	5.0 ± 2.4	39.6 ± 6.6	132.5 ± 12.1
1.6 ± 1.3	30.1 ± 5.8	351.3 ± 19.7	8888 ± 990	6433 ± 84	27.5 ± 5.5	10551 ± 108	1.9 ± 1.5	—	8.7 ± 3.3	288.2 ± 17.8
—	—	244.2 ± 19.4	346 ± 44.7	—	—	1969 ± 110	5.5 ± 2.9	—	15.9 ± 9.9	—
—	—	250.3 ± 16.6	124 ± 11.7	563 ± 25	—	1353 ± 39	—	—	0.3 ± 0.6	5.2 ± 2.4
—	—	81.1 ± 22.4	108.1 ± 25.8	—	—	2771.5 ± 131	16.4 ± 10.1	—	1171 ± 85	—
1.4 ± 1.9	5.4 ± 3.7	16.5 ± 6.5	138.3 ± 18.7	412 ± 32.2	2.4 ± 2.5	6554 ± 129	16.9 ± 6.5	16.2 ± 6.2	630.9 ± 40	1.7 ± 2.1
—	—	43.9 ± 16.5	329.7 ± 45.1	—	—	3029 ± 137	14.5 ± 9.5	—	1432 ± 94	—
—	6.2 ± 4.0	64.6 ± 12.8	89.8 ± 15.1	187 ± 21.8	1.7 ± 2.1	6593 ± 129	18.5 ± 6.9	30.4 ± 8.7	850.9 ± 46.5	2.4 ± 2.4
—	—	58.1 ± 18.9	71.7 ± 21.0	—	—	2634.3 ± 128	15.6 ± 9.8	—	1247 ± 88	—
1.1 ± 1.6	4.2 ± 3.3	46.9 ± 10.9	97.6 ± 15.7	212.7 ± 23.2	2.6 ± 2.6	4355 ± 105	16.0 ± 6.4	26.3 ± 8.2	644.6 ± 40.4	2.2 ± 2.4
0.7 ± 0.7	15.8 ± 3.1	102.5 ± 7.8	1163 ± 26	19186 ± 107	6.3 ± 1.9	24169 ± 120	14.0 ± 2.9	30.9 ± 4.3	1317 ± 27.9	52.6 ± 5.6
2.4 ± 1.6	8.8 ± 3.1	33.6 ± 6.1	4396 ± 70	14593 ± 1268	4.6 ± 2.3	35517 ± 1978	12.0 ± 3.6	15.9 ± 4.2	722.5 ± 28.2	32.9 ± 6.0
—	10.3 ± 2.5	40.4 ± 4.9	3932 ± 37.3	1663 ± 31.3	2.4 ± 1.2	32708 ± 139	—	—	32.0 ± 4.3	85.3 ± 7.1
0.6 ± 0.8	2.1 ± 1.7	50.1 ± 8.8	23210 ± 1891	5017 ± 88	—	30635 ± 2173	—	—	27.9 ± 6.6	511.9 ± 28.1
1.9 ± 1.2	39.6 ± 5.3	254.7 ± 13.3	1734 ± 34.8	2128 ± 38.6	3.0 ± 1.4	20621 ± 120	—	—	36.6 ± 5.1	65.5 ± 6.8
3.6 ± 2.0	4.5 ± 2.2	288 ± 17.8	20087 ± 1488	2981 ± 57	—	20907 ± 180	—	—	35.8 ± 6.3	38.0 ± 6.5
7.1 ± 2.1	38.0 ± 4.7	95.7 ± 7.5	2440 ± 38	601 ± 18.8	—	8623 ± 34.4	—	—	14.4 ± 6.6	136.8 ± 9.0
46.3 ± 20.6	18.1 ± 4.5	1196 ± 36.1	14397 ± 1259	2032 ± 47.3	—	12795 ± 1187	—	—	15.2 ± 4.1	79.5 ± 9.4

possibility may still exist. This is suggested from the high elemental levels observed at Fisherman's Wharf (copper and lead), Monterey Sewage Outfall (silver, cadmium, and zinc), and Elkhorn Slough (iron). These high values, possible consequences of pollution, should not go unchecked. Much study is still needed as to toxicity, base levels, and the possible biological magnification of heavy and trace metals.

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A New Species of *Primovula* from the Western Solomon Sea

(Gastropoda : Ovulidae)

BY

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(1 Plate)

INTRODUCTION

THE AUTHOR SURVEYED the reef mollusks of the Louisiade Archipelago in the Solomon Sea east of New Guinea, from November, 1969 to January, 1970. While I was on Nimoa Island, in the Calvados Chain, a violent cyclone struck which lasted for 4 days. By the end of that time, the beaches were heaped with organisms brought up from deep waters surrounding the fringing reef complex of the island. Many rare and unusual gastropods were found, including a remarkable ovulid. Further research proved it to be new to science and it is herein described.

MESOGASTROPODA

CYPRAEACEA

OVULIDAE FLEMING, 1828

Primovula THIELE, 1925

Primovula piriei Petuch, spec. nov.

Description: Shell cylindrically-fusiform, elongate, with crenulated and flaring terminals. Dorsum with numerous incised traverse striae and 12 spiral rows of evenly-spaced pittings which give the surface a slightly knobby appearance. The shoulder exhibits 6 prominent keel-like knobs. Base of shell flattened with a large, heavily-striated columellar area and a prominent toothed columellar lip. Labial lip flattened, with 56 denticles which become larger and more prominent towards the posterior end and extend over the shell margin. Columellar lip with 53 large uniform denticles. Shell light-weight and glossy, bright lavender pink in color with small brown fleckings. Aperture flaring at anterior end, but narrowing posteriorly.

Holotype: National Science Museum, Tokyo, Japan; NS MT-Mo 42254

Type Locality: Nimoa Island, Calvados Chain, Louisiade Archipelago, Solomon Sea; 11°16′ S; 153°15′ E.

Dimensions of Holotype: length 17.6 mm; width 6.2 mm

Distribution: This species appears to be endemic to the Louisiade Archipelago, but probably is found in other areas of the Solomon Sea, such as the Trobriand Islands. Another specimen was reportedly dredged from deep water off the Engineer Group, and is now in the collection of a person on Samurai Island, Eastern Papua, New Guinea.

Discussion: Although the shell was collected in very fresh condition on the beach, nothing remained of the animal for dissection. The author tentatively places this species in the genus *Primovula*, though there is a possibility of its belonging to the genus *Prosimnia* Schilder, 1927. This can only be cleared up by future collecting and dissection of this species. *Primovula piriei* bears some resemblance to *Prosimnia coarctata* (Adams & Reeve, 1848), but can easily be separated from that species by its larger size, more inflated aperture and shoulder knobs. It could also be confused with *Primovula striatula* (Sowerby 1st, 1828) but differs in aperture shape, by having the knobs and heavily denticulated columellar lip. It is a very unusual species and cannot be readily confused with any other form in the Ovulidae.

On the beach where *Primovula piriei* was collected, there had washed up large piles of gorgonians and other alcyonarians. It is possible that the species is associated with them, as is *Prosimnia* (CERNOHORSKY, 1968), and clung to them while they were torn from their holdfasts in deep water by the storm surf.

The species is named in honor of Dr. R. Gordon Pirie, Professor of Oceanography, Geology Department of the University of Wisconsin - Milwaukee, Milwaukee, Wisconsin.

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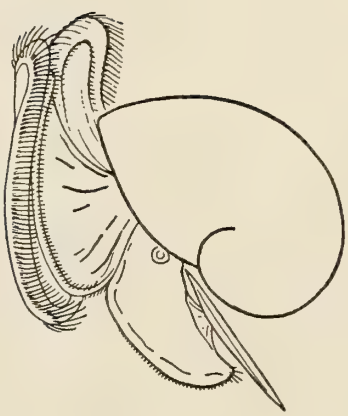

Figure *1* Figure *2*

Primovula piriei Petuch, spec. nov.
dorsal and ventral aspect of the holotype

Distribution and Natural History of Opisthobranch Gastropods from Las Cruces, Baja California del Sur, Mexico

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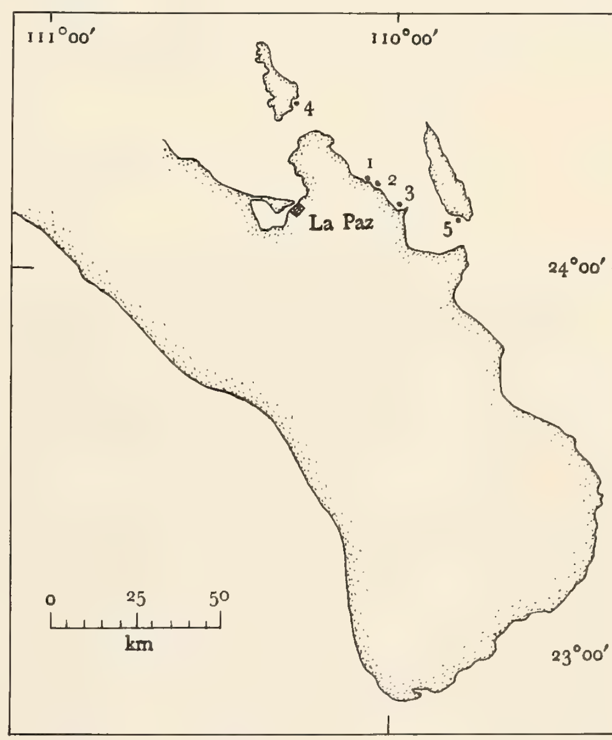
(2 Maps)

INTRODUCTION

THIS PAPER REPORTS the natural history and occurrence of 11 opisthobranch species found during July 20 to July 28, 1972, in the vicinity of the Las Cruces Biological Station, Baja California del Sur, Mexico. Habitat preferences, feeding, taxonomic and evolutionary considerations are given for some of the species.

Diving and collecting were done at 5 localities (Map 1): 1) Bahía Carisalito, 4 km north of the Station; 2) Bahía Las Cruces, the cove and bay immediately in front of the Station; 3) the bay north of Punta Gorda, 8 km south of the Station; 4) southeastern Isla Espíritu Santo, 36 km northwest of Las Cruces; and 5) the bay on the southwestern edge of Isla Cerralvo, 25 km southeast from Las Cruces.



Map 1

Southern tip of Baja California, Mexico, showing the five collecting localities of this study

SACOGLOSSA

ELYSIIDAE

Tridachiella diomedea (Bergh, 1894)

Six specimens of *Tridachiella diomedea* were obtained from Islas Espíritu Santo and Cerralvo, and from Bahía Carisalito. Five were between 8 and 25 mm in total length, and one was 43 mm long.

The type locality of *Tridachiella diomedea* is approximately 1.6 km off the western coast of Isla Cerralvo, at 24°11′N; 109°55′W, nearly $\frac{2}{3}$ the distance from Bahía

Las Cruces to my collecting locality on the southwestern edge of Isla Cerralvo.

Table 1

Latitude and Longitude of the Localities within the Gulf of California approximated to the nearest minute

Puerto Peñasco	31°18′ N; 133°35′ W
Puertecitos	30°21′ N; 114°38′ W
Puerto de Lobos (Cabo Tepoca)	30°16′ N; 112°51′ W
Puerto Refugio, Isla Angel de la Guarda	29°33′ N; 113°35′ W
Bahía de Los Angeles	28°53′ N; 113°30′ W
Isla Cedros (on the Pacific)	28°07′ N; 115°11′ W
Bahía San Carlos	27°56′ N; 111°04′ W
W. Isla San Francisco	24°50′ N; 110°35′ W
SE Isla Espíritu Santo	24°27′ N; 110°19′ W
Bahía Las Cruces	24°13′ N; 110°05′ W
SW corner Isla Cerralvo	24°09′ N; 109°49′ W

ANASPIDEA

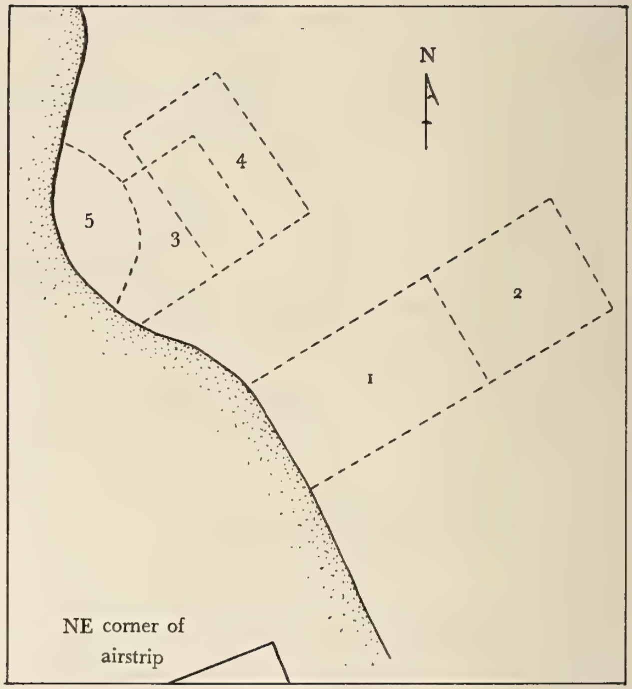
Aplysiidae

Stylocheilus longicauda (Quoy & Gaimard, 1824)

Although one of the most common opisthobranchs throughout the Gulf of California, *Stylocheilus longicauda* was first correctly reported as occurring in the Gulf just over 6 years ago (Farmer, 1967). Prior to this, it was reported as *Notarchus (Aclesia)* sp. (Steinbeck & Ricketts, 1941) and as *Aclesia rickettsi* MacFarland, 1966. Engel & Hummelinck (1936) and Roller (1970) list the synonyms of *S. longicauda.*

Stylocheilus longicauda characteristically occurs intertidally, among tidepools, or in shallow subtidal depths on various kinds of seaweeds (Quoy & Gaimard, 1824; Pease, 1860; Ostergaard, 1955; Marcus & Marcus, 1963; Kay, 1964; Bertsch, 1970). It also occurs on rocky or sandy substrate (Kay, *op. cit.*; Farmer, 1967).

Since there is little knowledge about its ecology, I studied the intertidal and subtidal region at the southern end of Bahía Las Cruces in order to find out if *Stylocheilus longicauda* shows a preference for a particular habitat. I chose this study area (immediately west of the Las Cruces airstrip) because of its accessibility, the ease with which quadrats could be measured and quantitative data gathered, the large numbers of *S. longicauda* living in this general region, and the diversity of habitats within a small area. Variables, such as fluctuations in water temperature and wave action, were negligible, thus reducing factors



Map 2

Sketch of southern tip of Bahía Las Cruces, showing the transect sites studied to determine the habitat preference of *Stylocheilus longicauda*

that might cause different population densities of *S. longicauda* at the study site. The study was conducted within the 2-day period of July 20-21, 1972, to eliminate seasonal fluctuations, and within the same time period each afternoon (between 1300 and 1600 hours) to minimize any differences that may exist in diurnal activity periods.

The area was divided into 5 quadrat regions (Map 2).

Region 1 was a rocky intertidal region, covered by 30 to 75 cm of water during the study period. It extended from 5 to 14 m from the shoreline. A unicellular blue-green alga was growing on the rocks. It formed a thin, sparse layer over the rocks, making them very slippery. There were no diatoms nor other organisms encrusting this alga.

Region 2 consisted of the subtidal area immediately beyond region 1, and had the same kind of alga. However, the rocks were 1.0 to 1.5 m below the water surface, and the area, starting at 15 m, extended to 25 m from the shore. This area was readily separable from area 1 in the

field, because 2 species of echinoderms occurred in it and not in the first area: *Ophiocoma aethiops* Lütken (the blunt-spined brittle star) and the long-spined urchin, *Diadema mexicanum* Agassiz.

Region 3 was situated 33 m northwest of quadrats 1 and 2, and was sampled 6 to 10 m from shore. It consisted of a rocky and sandy substrate, covered by dense growths of a trabeculated alga (*Caulerpa* cf. *C. pinnata*) with flattened, pinnate branches.

Region 4 consisted of an area of *Polysiphonia* algal growths overlapping locality 3. The algal masses served to readily distinguish the quadrat regions. Area 4 was in 1 m of water, 6 to 14 m from shore, with a rocky substrate.

Region 5 was a circular area, distinguished by a sandy substrate, 1.0 to 1.5 m deep, surrounded by region 3 seaward, and by the shore westward. The *Caulerpa* alga from region 3 was scattered throughout region 5, with shoots spreading out from the rocks and across areas of bare sand.

Table 2

Frequency of Occurrence of *Stylocheilus longicauda* in five different habitats

Transect number	Total size of area examined (in cm²)	Number of specimens of *Stylocheilus* found	Number of rocks or algae clumps examined
1	5202	0	18
2	5300	0	18
3	7350	53	13
4	4750	85	18
5	10125	61	5

The algae from areas 3, 4, and 5 were heavily encrusted with diatoms. The most common species were *Licmophora abbreviata* Agardh, 1831 (60% of the diatoms), and *Grammatophora oceanica* (Ehrenberg, 1854) Grunow, 1881 (comprising about 10% of the diatom specimens).

Measurements of areas and counts of number of specimens of *Stylocheilus longicauda* occurring in each of the 5 quadrat regions were made *in situ* by snorkel diving. During the day, *S. longicauda* actively crawls over the surface of rocks and algae, permitting easy counting of specimens with little disturbance to the habitat.

Rocks covered by the 3 kinds of algae were randomly chosen, their length measured with a ruler, and then the number of *Stylocheilus longicauda* occurring on the algae was recorded. The squares studied in region 5 were randomly chosen areas of sandy bottom; distances were measured by a ruler, and the specimens occurring within each square were counted.

The total area studied in regions 1 to 4 was approximated by considering the width of the rock or algal mass as $\frac{2}{3}$ its total length. These figures were rounded off to the nearest centimeter for area determination and then added together to give the total area sampled in each quadrat.

Table 3

Density of *Stylocheilus longicauda* Within the Five Different Habitats

Transect number	Density
1	0 per 5202 cm²
2	0 per 5300 cm²
3	1 per 140 cm²
4	1 per 55 cm²
5	1 per 170 cm²

The results of this study are given in Tables 2 and 3. There is a definite correlation between the kind of alga and the relative abundance of *Stylocheilus longicauda*. Thick, dense mats of algae, covered with large amounts of diatoms (as in regions 3, 4, and 5) are a preferred habitat for *S. longicauda* in the Las Cruces area. There is an extremely low occurrence of *S. longicauda* in areas that do not exhibit their preferred habitat's characteristics.

Observations that I have made in other parts of the Gulf of California strengthen the predictive value of the observed low abundances of *Stylocheilus longicauda* outside its characteristic preferred habitat.

While diving on the western side of Isla San Francisco on July 8 and 9, 1969, I found only 2 specimens of *Stylocheilus longicauda* (see Bertsch, 1970). The algal covering on the rocks was similar to that encountered in quadrat regions 1 and 2, and the extremely low density of *S. longicauda* was comparable with that found in this study for that habitat.

During the last week of March, 1972, Gary and Scott Williams, Terrence Gosliner, Mark Noonan, Tim Elliott, and I collected 18 species of opisthobranchs from Puertecitos. No specimens of *Stylocheilus longicauda* were found, and no dense algal growths occurred at our collecting sites.

Other collecting that I did for this report yielded only 5 specimens of *Stylocheilus longicauda*. They were all

found together, under a rock, in 3 m of water, just north of Punta Gorda. The alga in this locality was similar to that found in regions 1 and 2, and the density of *S. longicauda* was not comparable with the numbers found in the dense algal growths at regions 3, 4, and 5. The collecting sites on southeast Isla Espíritu Santo and southwest Isla Cerralvo yielded no specimens of *S. longicauda.* This was predictable because neither locality had extensive, dense algal masses.

Feeding was observed in the field (in quadrat regions 3, 4, and 5) and in the laboratory. When feeding, *Stylocheilus longicauda* crawls over the alga and scrapes off the diatoms, which it consumes. An earlier report (Bertsch, 1970) that *S. longicauda* ate fronds of *Spyridia filamentosa* (Wulfen) Harvey, should be corrected to read that this animal eats the diatoms on *Sp. filamentosa. Stylocheilus longicauda* did not appear to be selective among the various diatoms on the alga. Since 2 species of diatoms on the algae comprised 70% of that population, the major food items that *S. longicauda* ate in the area studied were the diatom species *Licmophora abbreviata* and *Grammatophora oceanica.*

While feeding, the opisthobranchs continued crawling forward, everting the radula from the mouth (at which time it was readily visible to the naked eye), then retracting the radula with a slight upward jerk of the head. Radular strokes were quite rhythmic and rapid, often more than 1 per second. The animals expelled fecal pellets while eating.

NOTASPIDEA

Pleurobranchidae

Berthellina engeli Gardiner, 1936

A total of 5 specimens of *Berthellina engeli* were found, 1 from SE Isla Espíritu Santo, 1 from SW Isla Cerralvo, and 3 from Bahía Carisalito. The small specimens, between 10 and 20 mm in length, were all found on the underside of rocks. The negative phototaxis of *B. engeli* has already been reported (Bertsch, 1970).

NUDIBRANCHIA

Doridoida

Chromodorididae

Species of the genera *Chromodoris* Alder & Hancock, 1855, and *Hypselodoris* Stimpson, 1855, occur quite commonly throughout the Gulf of California. However, in two separate research visits to the Las Cruces region, I have observed a great variability in their abundance (Table 4). In July, 1969, 7 specimens of two species of *Chromodoris* were obtained during the period of an entire month from 28 collecting dives lasting 2 to 3 hours each. In July, 1972, a total of 31 specimens of 4 species of *Chromodoris* and *Hypselodoris* were obtained during a one-week period (July 20 to 26) from 7 collecting dives, lasting 2 - 3 hours each. The more than 400% increase in the occurrence of these animals emphasizes the unpredictable seasonality characteristic of many nudibranch species.

Table 4

Comparative Abundance of Four Species of Chromodorids in the years 1969 and 1972 in the Las Cruces region

Species	Number of specimens				Total specimens	
	Las Cruces		Isla Cerralvo			
	1969	1972	1969	1972	1969	1972
Chromodoris baumanni	0	1	0	0	0	1
Chromodoris norrisi	5	16	1	1	6	17
Chromodoris sedna	0	2	1	3	1	5
Hypselodoris sp.	0	8	0	0	0	8
Totals:	5	27	2	4	7	31

Chromodoris baumanni Bertsch, 1970

One 37 mm long specimen of *Chromodoris baumanni* was collected subtidally at Bahía Carisalito. By close examination (900 ×) of the "gelatinous" integument, I found long, thin, rod-like spicules scattered throughout the tissue. Marcus & Marcus (1967) previously reported that this species has no spicules.

Chromodoris norrisi Farmer, 1963

Both in July, 1969, and July, 1972, *Chromodoris norrisi* was the most frequently encountered chromodorid. It was typically found crawling on the sides or tops of rocks, in the sunlight. Sixteen specimens were measured, varying in total length from 21 to 46 mm; the median length was 28 mm.

Chromodoris sedna (Marcus & Marcus, 1967)

Five specimens of *Chromodoris sedna* were collected, varying in length from 13 to over 40 mm.

Hypselodoris sp.

Eight specimens of an undescribed *Hypselodoris* were found subtidally at the Las Cruces area – one at Bahía Carisalito, one at Las Cruces, and 6 just north of Punta Gorda. The largest specimen measured 57 mm long. I have also seen this species intertidally at Puertecitos (a

69 mm specimen, collected by Scott Williams on March 27, 1972).

The species of *Hypselodoris* from tropical west America are poorly known. Within the same year, *Hypselodoris agassizii* (Bergh, 1894) was synonymized with *H. californiensis* (in Keen, 1971), and re-instated as a separate, valid species (Sphon, 1971) on the basis of external coloration. A third species, *H. aegialia* (Bergh, 1904), is known only from the type material.

The coloration of *Hypselodoris californiensis* is deep blue, with large yellow dots or streaks on the body. Sphon (1971) considers "a single, continuous yellow stripe along the border of the mantle" to be diagnostic. This stripe is apparently mentioned in the original description of *H. californiensis*: "A brighter, fine line seemed to border the margin of the mantle-edge and that of the foot" (Bergh, 1879), but it is not clear as to just what color Bergh considered the stripe. In his work on the "*Albatross*" material, Bergh (1894) mentions no yellow stripe on *H. californiensis*. Moreover, Cockerell (1902), Cockerell & Eliot (1905), and MacFarland (1966) described a light blue or white marginal stripe.

The coloration of the mantle edge of *Hypselodoris californiensis* varies. A single, light yellowish, white, or pale blue stripe encircles the edge of the mantle. *Hypselodoris agassizii* can be distinguished by its multiple green and white marginal striping, and *H. aegialia* is green with whitish flecks.

Polyceridae

Polycera alabe Collier & Farmer, 1964

The recorded range of *Polycera alabe* is from its type locality in the Pacific (Isla Cedros) to the northern end of the Gulf of California (Keen, 1971). In the Gulf of California it has been found at Puertecitos (pers. observ., March, 1972), Puerto de Lobos (Farmer, 1971), Puerto Refugio (Collier & Farmer, 1964), and Bahía San Carlos (Williams & Gosliner, 1971). The reported range of *P. alabe* consists of two disjunct sites: off the Pacific coast of Baja California, and in the northern part of the Gulf of California.

On July 24, 1972, I collected 5 4 - 5 mm long specimens of *Polycera alabe* from a cove on the southeastern side of Isla Espíritu Santo. This extends the known range of *P. alabe* 400 km to the south, and establishes an intermediate occurrence for this species between its two previously isolated populations. The distribution of *P. alabe* is now throughout the Gulf of California, and on the Pacific coast of Baja California to Isla Cedros.

Dendrodorididae

Dendrodoris krebsii (Mörch, 1863)

Two days after I left Las Cruces, on July 28, 1972, Andrew Toepfer and Gene Lombard found one specimen of *Dendrodoris krebsii* on the underside of a rock at Bahía Carisalito. The surface of the rock was covered with the encrusting coralline alga *Lithothamnion* sp. The preserved *D. krebsii* measures 25 mm in length.

Dendrodoris krebsii has been previously recorded from nearby Bahía La Paz (Collier & Farmer, 1964). This species is known to occur throughout the Panamic province north of Tenacatita, Jalisco (19°17′N; 104°54′W), and throughout the Caribbean faunal area from Florida, U. S. A., to Cananeia, Brazil (Marcus & Marcus, 1967).

Dendronotoida

Bornellidae

Bornella sp.

On July 26, 1972, Thomas S. Cooke and Gary Stellern found 6 specimens of a new species of *Bornella* under rocks in 3 to 4 m of water at Bahía Carisalito. No genera of the family Bornellidae Fischer, 1883, have previously been reported from any part of the Pacific coast of the Americas.

All known species of the genus *Bornella* occur in tropical provinces. Nine were described in the Indo-West Pacific region from the coasts of Africa and Saudi Arabia to Japan and the Society Islands (Tahiti), 1 from St. Thomas in the Caribbean, and 1 has an unknown type locality (Russell, 1971).

The closely related family Dendronotidae Sars, 1878, is largely restricted to north temperate and arctic seas (Robilliard, 1970). The only exceptions to this are 2 specimens of *Dendronotus gracilis* Baba, 1949, collected from 9 - 24 m in New Zealand waters (Robilliard, *op. cit.*), and the Panamic species *Dendronotus nanus* Marcus & Marcus, 1967. The close relationship between these two families can be explained on the basis of perhaps polyphyletic radiations from an ancestral bornellid-like group in the tropics, with one or more dispersals northward that lost the ceratal gills and evolved into the *Dendronotus* group, and adaptive radiations throughout the tropics that have given rise to the numerous species of *Bornella*.

Dotidae

Doto lancei Marcus & Marcus, 1967

The recorded sites where *Doto lancei* has been observed are all in the northern part of the Gulf of California, both on the Sonoran and Baja Californian coastlines. The type locality is Puerto Peñasco (Marcus & Marcus, 1967). Additional animals have been reported from Puerto de Lobos (Farmer, 1971), Bahía de Los Angeles (Keen, 1971), and Bahía San Carlos (Williams & Gosliner, 1971; also personal observations, December, 1970).

On July 25, 1972, while diving at the southwestern corner of Isla Cerralvo, I found specimens of *Doto lancei* crawling on *Aglaophenia*. Egg masses of *D. lancei* (Type A as described by Hurst, 1967) were seen on the fronds of the hydroid, and the nudibranchs were seen either on the fronds or crawling on the base of the stem.

Five specimens were collected and preserved. The largest specimen measured 7 mm in length when alive, and had 8 pairs of cerata, with 5 rows of ceratal tubercles and one apical tubercle. The proximal tubercles were specked with white dots, whereas each distal tubercle possessed a subapical black ring and a black apical spot.

This collection represents a southward range extension for *Doto lancei* of 442 km. The known range of *D. lancei* is now throughout the entire Gulf of California.

DISCUSSION ON DISTRIBUTIONAL RECORDS

The ranges of nudibranchs in tropical West America are confusing and little known. Over 15 species are known only from isolated locations on the northern Pacific coast of Baja California and in the northern part of the Gulf of California. Another 12 species are recorded only from the northern Gulf and 10 or more have been collected only in the vicinity of Panama Bay. Such scattered data and disjunct occurrence records admittedly result from the little amount of work that has been done on the nudibranch populations of tropical West America.

Data reported from this collection have extended the ranges of two nudibranch species throughout the Gulf of California. These range extensions and others (Bertsch, 1971; Ferreira, 1972; Ferreira & Bertsch, 1972; Sphon, 1972) need to be placed in a more comprehensive perspective. Those Panamic species with currently disjunct populations may eventually prove to have continuous ranges, similar to *Polycera alabe, Dendrodoris krebsii, Armina californica* (Cooper, 1862), *Spurilla chromosoma* Cockerell & Eliot, 1905, and other species with continuous ranges on both sides of the Baja California peninsula. Those species with extremely narrow ranges (based only on type material or a few scattered collections) possibly will be found along a wider latitudinal range within the Panamic province, similar to such widely distributed species as *Chromodoris baumanni, Ch. sedna, Doto lancei,* and *Flabellina telja* Marcus & Marcus, 1972. These hypotheses are consistent with the continuous ranges of many Panamic species (Keen, 1971) and with statistical analyses of the north-south length of nudibranch ranges within the Panamic province (Bertsch, 1973).

These remarks, however, are made only in view of other possible hypotheses: the ranges of the species may be disjunct presently (having at one time been continuous), the disjunct populations may be different species, and some species may be naturally rare with narrow ranges. Insufficient data from recent material, capricious taxonomy, and the lack of a fossil record, limit our current understanding of Panamic nudibranch distributions.

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Range Extensions for Four Sacoglossan Opisthobranchs from the Coasts of California and the Gulf of California

(Mollusca : Gastropoda)

BY

GARY C. WILLIAMS[1] AND TERRENCE M. GOSLINER[2]

(2 Maps)

INTRODUCTION

Six opisthobranch species of the order Sacoglossa have previously been recorded from coastal California and 9 species from the Gulf of California. The present report establishes the total number of sacoglossans reported from California to be 7 and the total number from the Gulf of California to be 10. The ranges of two other species are extended within their respective provinces. The sacoglossan opisthobranchs from the California and Gulf coast are listed, together with their known geographic ranges, as follows:

Sacoglossans from California

1. *Alderia modesta* (Lovèn, 1844)
   San Juan Islands, Washington, to Elkhorn Slough, California; Europe
2. *Elysia hedgpethi* Marcus, 1961
   =*Elysia bedeckta* MacFarland, 1966
   San Juan Islands, Washington, to Bahía de los Angeles and Puertecitos, Baja California to Bahía de San Carlos, Sonora
3. *Hermaea vancouverensis* O'Donoghue, 1924
   Vancouver Island, Washington to Bodega Harbor, California
4. *Hermaea oliviae* (MacFarland, 1966)
   Duxbury Reef, California to Monterey Bay, California
5. *Hermaeina smithi* Marcus, 1961
   = *Phyllobranchopsis enteromorphea* Cockerell & Eliot, 1905 *in* MacFarland, 1966
   San Juan Islands, Washington to San Diego, California and Bahía de San Carlos, Sonora
6. *Placida dendritica* (Alder & Hancock, 1843)
   = *Hermaea ornata* MacFarland, 1966
   Bodega Head, California to Newport Bay, California
7. *Stiliger fuscovittatus* Lance, 1962
   San Juan Islands, Washington to San Diego, California and Bahía de los Angeles, Baja California

Sacoglossans from the Gulf of California

1. *Berthelinia chloris* (Dall, 1918)
   = *Berthelinia belvederica* Keen & Smith, 1961
   Bahía Ballenas, Punta Abreojos to La Paz, Baja California
2. *Cylindrobulla californica* Hamatani, 1971
   Isla Espiritu Santo, Bahía San Gabriel, Baja California
3. *Elysia hedgpethi* Marcus, 1961
   San Juan Islands, Washington to Bahía de los Angeles and Puertecitos, Baja California, and to Bahía de San Carlos, Sonora
4. *Elysia vreelandae* Marcus & Marcus, 1970
   San Agustin, Sonora, Mexico
5. *Hermaea hillae* Marcus & Marcus, 1967
   Puerto Peñasco, Sonora, Mexico
6. *Hermaeina smithi* Marcus, 1961
   San Juan Islands, Washington to San Diego, California and Bahía de San Carlos, Sonora

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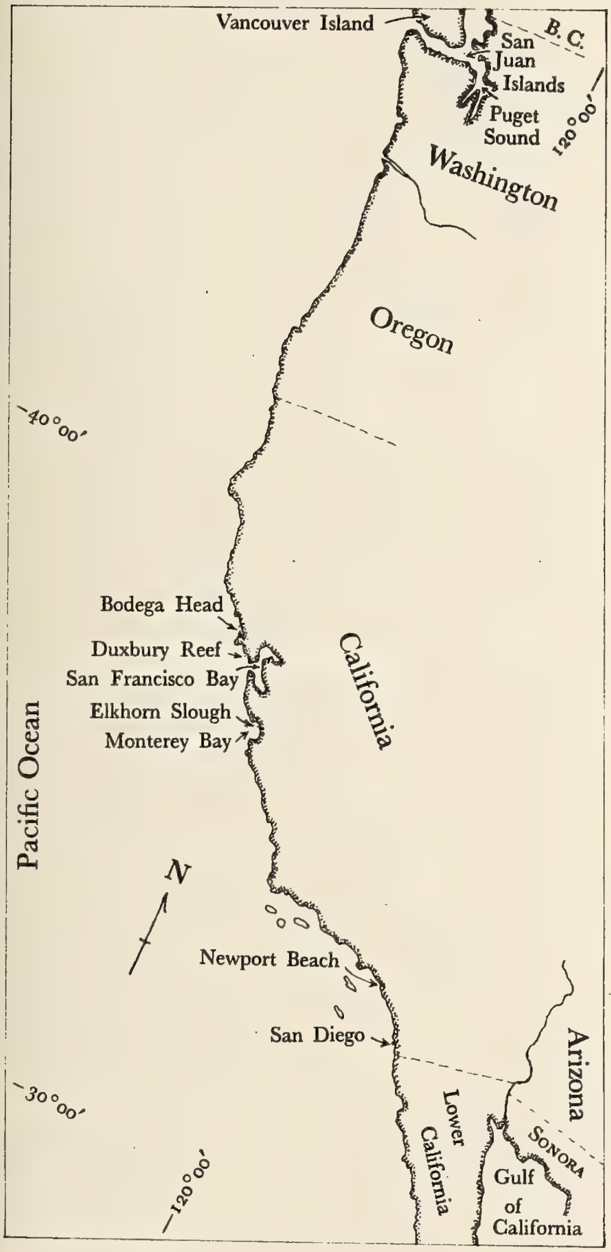
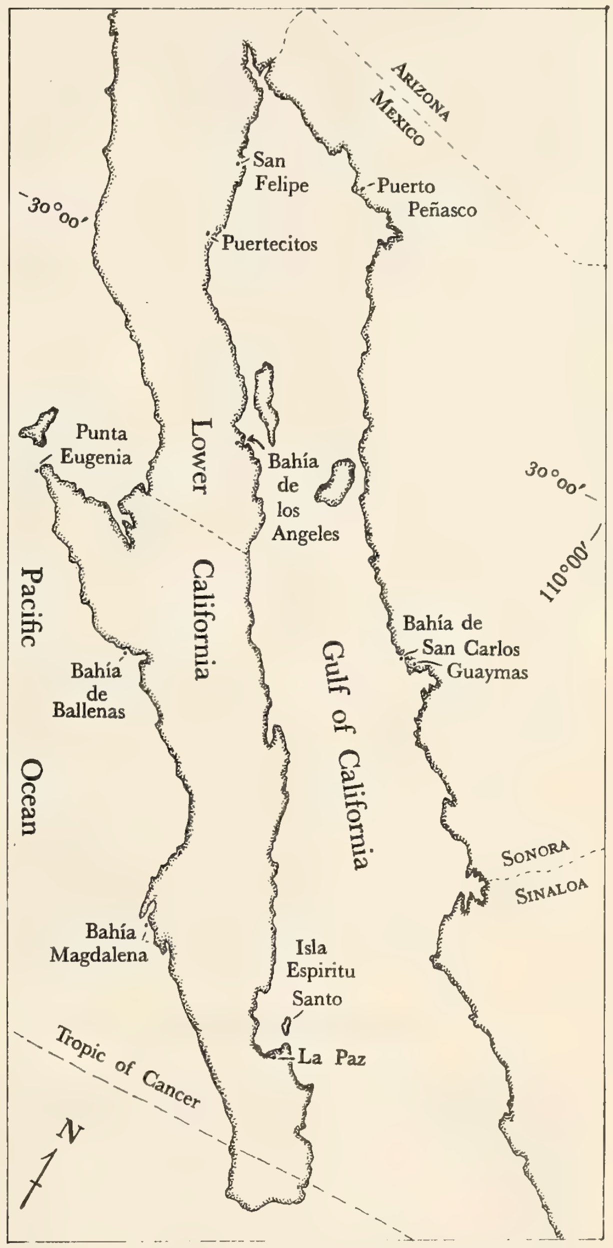


Map of California



Map of Lower California

7. *Julia thecaphora* (Carpenter, 1857)
= *Julia equatorialis* Pilsbry & Olsson, 1944
La Paz, Baja California to Peru

8. *Oxynoe panamensis* Pilsbry & Olsson, 1943
Southern end of the Gulf of California to Panama Bay

9. *Stiliger fuscovittatus* Lance, 1962
San Juan Islands, Washington to San Diego, California and Bahía de los Angeles, Baja California

10. *Tridachiella diomedea* (Bergh, 1894)
Throughout the Gulf of California to Panama

Elysia hedgpethi Marcus, 1961

The elysiacean sacoglossan *Elysia hedgpethi* has been recorded by MARCUS (1961) at the type locality in Tomales Bay and MACFARLAND (1966) from Monterey Bay (as *E. bedeckta*). KEEN (1971: 817) records the range of the species as from Puget Sound, Washington to Bahía de los Angeles, Baja California.

In December of 1970, we observed 3 individuals of this species in the exposed intertidal lava pools near the mouth of Bahía de San Carlos, Sonora, Mexico. On March 28, 1972, 12 individuals were observed in the intertidal rocky region just north of Puertecitos, Baja California. On both occasions the animals were observed on the chlorophyte alga *Codium* sp. The citing at Puertecitos represents a northern range extension inside the Gulf of California of approximately 150 miles (240km). The citing at Bahía de San Carlos establishes the species on the eastern shores of the Gulf of California. The newly established range of *Elysia hedgpethi,* thus, is from Puget Sound (San Juan Islands), Washington to Bahía de los Angeles and Puertecitos, Baja California, and to Bahía de San Carlos, Sonora.

The animals collected from the Sea of Cortez were quite small (under 6mm in length). The species is distinguished by its large, thin, undulating parapodia, greenish coloration, auriculate rhinophores, and severely flattened body when the parapodia are extended downward.

One other species of *Elysia* Risso, 1818 is known from the Gulf of California: *E. vreelandae* Marcus & Marcus, 1970, known only from the type locality, San Agustin, Sonora, Mexico. It is described (MARCUS & MARCUS, 1970: 194) as being "a small, dark olive-green species with lighter borders of the parapodia and blue dots."

Hermaea vancouverensis O'Donoghue, 1924

The small sacoglossan *Hermaea vancouverensis* has been recorded previously only in the original description from the type locality, the Vancouver Island region, British Columbia, Canada.

On July 7, 1971, while we were observing the fauna of the *Zostera marina* (Linnaeus, 1756) environment in Bodega Harbor, Sonoma County, California, egg masses which appeared to be those of an opisthobranch were seen on the blades of *Zostera.* Closer examination yielded many specimens of a small, dark green sacoglossan which proved to be *Hermaea vancouverensis.*

It was later discovered that *Hermaea vancouverensis* had been feeding on the epiphytic diatom *Isthmia nervosa* which abounds on the *Zostera* leaves. O'DONOGHUE (1924) notes that *H. vancouverensis* is found on *Zostera* and presumably feeds on epiphytic diatoms.

On July 20, 1971 additional field observations were made at the same locality. In a square meter sample over 75 individuals of *Hermaea vancouverensis* were counted. While this estimate does not pretend to be random or statistically valid, it does give some idea as to the relative abundance of this sacoglossan at that particular time. Additional observations made in January of 1972 yielded no individuals although *Isthmia* was seemingly more abundant. No factor accountable for the complete absence of the population could be discerned.

On March 5, 1972, 2 individuals of *Hermaea vancouverensis* were found on *Isthmia nervosa* in the open coastal environment of Coleman State Beach, Sonoma County, California, just a few kilometers north of Bodega Harbor. On May 16, 1972, a single animal was found in the same locality. These findings are significant since *H. vancouverensis* has not previously been recorded from the rocky intertidal environment.

The occurrence of *Hermaea vancouverensis* in the Bodega Bay region is of particular zoogeographical significance, as its presence in Bodega Harbor and at Coleman Beach represents a southern range extension of well over 900 miles (1440km).

In external appearance *Hermaea vancouverensis* is quite similar to *H. oliviae* (MacFarland, 1966). MARCUS & MARCUS (1967: 154) reassigned *H. oliviae* from *Hermaeina* to *Hermaea* based on radular tooth shape. Both species have a light yellowish-white ground color with dark green stippling around the dorsal surface. The main external differences between the two species are the yellow-tipped cerata in *H. oliviae* as contrasted with the lack of a differentially colored ceratal apex in *H. vancouverensis.* The cerata in *H. oliviae* are very regular in shape as contrasted to the quite irregularly shaped cerata of *H. vancouverensis.* Internally the differences between the two species are quite marked. The radular teeth of *H. oliviae* have many denticles while those of *H. vancouverensis* are smooth and lack any denticulation.

On the basis of spindle-shaped rhinophores in *Hermaea vancouverensis,* MARCUS & MARCUS (1967: 153) have transferred the species to the genus *Stiliger.* However, the rhinophores are auriculate as in more typical members of the Sacoglossa and therefore the question of generic assignment should be investigated further.

Hermaeina smithi Marcus, 1961

The sacoglossan opisthobranch *Hermaeina smithi* has previously been known from the San Juan Islands, Washington to San Diego, California. ROLLER & LONG (1969) report the species as being frequent at Cayucos, Hazard Canyon, and Shell Beach in San Luis Obispo County,

California, GOSLINER & WILLIAMS (1970) report it as being a frequent animal in the intertidal pools of Duxbury Reef in Marin County, California. GONOR (1962: 86) records the species from several localities in the Puget Sound area of Washington, along with the following California stations: La Jolla, Newport Bay, Bolinas, Tomales Bay, and Bodega Bay.

On December 24, 1970, two individuals of *Hermaeina smithi* were observed at Bahía de San Carlos, Sonora, Mexico on the eastern side of the Gulf of California (Lat. 27°55′N; Long. 111°05′W). The animals were crawling on the chlorophyte alga *Enteromorpha* sp., in the shallow pools of the intertidal mudflats at low tide.

This citing represents the first known record of *Hermaeina smithi* south of San Diego and the first record of the genus and species in the Gulf of California and well into the Panamic province. It represents a southward range extension of approximately 5 degrees of latitude. The newly established range of the species, thus, is from San Juan Island, Washington to San Diego, California and to Bahía de San Carlos, Sonora. No intermediate stations between San Diego and Bahía de San Carlos have been reported as yet.

The animals from Sonora are externally very similar to Pacific coast specimens collected in recent years. The 2 individuals observed measured 9 mm and 12 mm in length, respectively. They can be characterized by their very dark to almost black body coloration interrupted with patches of cream-white at the bases of the cerata, tips of the rhinophores, and eye regions of the head. The rhinophores are elongate auriculate, characteristic of the sacoglossans and distinguishing this species from the eolid nudibranchs. Otherwise, the cerata and general body shape closely resemble that of some eolids and the species may be mistaken for an eolid on superficial observation.

Two other species of the family Hermaeidae have been recorded from the Gulf of California: *Hermaea hillae* Marcus & Marcus, 1967, from the type locality, Puerto Peñasco, Sonora, Mexico, and *Stiliger fuscovittatus* Lance, 1962, from Bahía de los Angeles on the western side of the Gulf.

Placida dendritica (Alder & Hancock, 1843)

This small green sacoglossan has been reported from Monterey Bay, California by MACFARLAND, 1966. LONG (1969) synonymized *Hermaea ornata* MacFarland, 1966 with *Placida dendritica* Alder & Hancock, 1843. In the same paper LONG established the geographical range of the species as from Pismo Beach in San Luis Obispo County, California to San Francisco Bay. GOSLINER & WILLIAMS (1970) extended the range further southward, recording the species from San Francisco Bay to Newport Beach, Orange County.

During June and July, 1971, the authors collected numerous individuals of *Placida dendritica* from the outer coast of Bodega Head in Sonoma County, California (Lat. 38°18′N; Long. 123°04′W). The animals were found in the rocky intertidal zone of this region crawling on the siphonalean chlorophyte alga *Codium fragile* (Suringar) Hariot. LONG (1969: 10) and MACFARLAND (1966: 400) report the animal on *Bryopsis,* also a siphonalean chlorophyte, which is a frequently encountered alga in the bay boat landings and shores of California. The newly established range of *Placida dendritica* is Bodega Head, Sonoma County to Newport Beach, Orange County, California. The occurrence of this species in the Bodega Bay region constitutes a northward range extension of approximately 60 miles (*ca.* 100 km).

The individuals of *Placida dendritica* collected from the Bodega Bay region did not exceed 7 mm in length. The species can be distinguished by the elongate, auriculate rhinophores and yellowish to whitish body color with green cerata and green mottling around the sides and top of the head, rhinophores, and caudal region. Because of its overall green coloration, the animal is usually difficult to distinguish from the similarly colored *Bryopsis* and *Codium,* the two algal substrata upon which *Placida* is usually found.

On May 14, 1972 we observed 12 individuals of *Placida dendritica* on *Codium fragile* in the lower zone exposed tide pools of Duxbury Reef, Marin County, California. This represents another collecting station within the newly established range of the animal.

ACKNOWLEDGMENTS

Our thanks are expressed to those who aided extensively in field observations, especially Scott Williams, Michael Gosliner, and Hans Bertsch.

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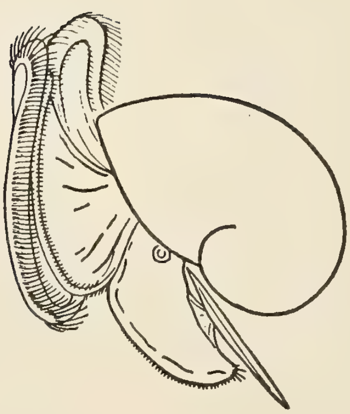

NOTES & NEWS

Sterkia hemphilli (Sterki) in Central California

BY

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THE MINUTE PUPILLID SNAIL *Sterkia hemphilli* (Sterki, 1890) enjoys a fairly wide latitudinal distribution in southern and Lower California. It has been reported in coastal and subcoastal situations from Punta Abreojos north to the San Diego region (PILSBRY, 1948) and inland in Waterman Canyon, San Bernardino Mountains, San Bernardino County (BERRY, 1916).

In October 1972 the author collected vegetable debris from under plant clumps on sand dunes immediately north and west of Oso Flaco Lake, southwestern San Luis Obispo County. *Sterkia hemphilli* was present in the debris in considerable numbers.

The specimens agree in most particulars with original lot material in the California Academy of Sciences and with specimens from Waterman Canyon (A. G. Smith collection No. 883). The peripheral sulcus on the last whorl is consistently well developed. Two scalariform specimens were found, one of $2\frac{1}{2}$, the other of $3\frac{1}{2}$ whorls. Variable characters within the species include the strength of the peripheral sulcus, convexity of whorls, and length-breadth ratio.

This portion of the central California coast has a mild climate with cool summers and relatively uniform temperatures. Most of the year's rainfall occurs in winter. At the collection site, the vegetation is the Coastal Strand plant community of MUNZ & KECK (1959); conspicuous plants include sea-fig (*Carpobrotus chilensis*), Hottentot-fig (*C. edulis*), coastal isocoma (*Isocoma veneta*), prickly phlox (*Leptodactylon californicum*), and bush lupine (*Lupinus* spp.). Around the roots of these plants the sand is somewhat stabilized. Coastal fog condenses on the foliage; a drip zone underneath offers slight continual dampness throughout the rainless summer months. This undoubtedly favors molluscan activity.

In addition to *Sterkia hemphilli,* the minute snails *Striatura pugetensis* (Dall, 1895), *Punctum conspectum* (Bland, 1865), and *Vertigo californica californica* (Rowell, 1861) were found in the litter. Shells of an *Helminthoglypta* similar to *H. walkeriana* (Hemphill, 1911) were common on top of the debris.

The author extends his thanks to Allyn G. Smith, California Academy of Sciences, who examined the material and recognized the occurrence as a range extension. Elizabeth McClintock kindly identified some of the plant species. Representative specimens of the snail have been deposited in the Department of Geology, California Academy of Sciences, and in the private collections of A. G. Smith and the author.

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Babakina, New Name for *Babaina* Roller, 1972, Preoccupied

BY

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RECENTLY SEVERAL COLLEAGUES have kindly informed me that the generic name *Babaina* has been listed in the systematic section of the work on the subclass Opisthobranchia, family Chromodorididae by FRANC (1968) in the Traité de Zoologie. The name is attributed to Odhner, but apparently first appears in the Franc work, with no statement as to how the name was first proposed, or who made the type choice. The full citation from page 867 is as follows:

"*Babaina* Odhner. Dents toutes allongées, étroites, bicuspidées. *B. florens* Baba, Japon."

It would appear that the description by Franc is sufficient to constitute a valid generic name. Therefore the

Babaina proposed by me (ROLLER, 1972) for a genus of eolid nudibranchs is preoccupied. I propose the name ***Babakina*** as a substitute for *Babaina* Roller, 1972. The new family name would become **Babakinidae**.

BABAKINIDAE Roller, nom. nov.

Babakina Roller, nom. nov.

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METHODS & TECHNIQUES

A Method for Marking Nudibranchs

BY

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INTRODUCTION

Many of the published methods for marking invertebrates depend on the presence of a hard exoskeleton or shell (Southwood, 1966). These methods are not practical for use on nudibranchs which are covered externally with a fleshy mantle. South (1965) was able to mark the slug *Agriolimax reticulatus* by feeding the animals on agar jelly with 0.2% neutral red. The darkly stained digestive glands of these slugs were visible through their feet. Although this technique is probably applicable for the group marking of some nudibranchs, the intense pigmentation of other species, such as *Rostanga pulchra* MacFarland, 1905, may render it impractical.

During a study of the behavior and ecology of the dorid nudibranch, *Rostanga pulchra* (Anderson, 1971), several methods were tried to mark individual animals so that they could be followed from day to day in the field. This paper will report on the varied success of the 3 marking methods used.

MATERIALS and METHODS

The field experiments were done at the Great Tide Pool near Point Pinos, Pacific Grove, California, during periods of low tides. A detailed map of the study area, showing the exact locations at which the nudibranchs were found, was made to facilitate recovery. "Recovery" involved noting the location and behavior of the animals of interest and immediately returning them to the substrate on which they were found.

Three marking methods were tested: Some nudibranchs were marked by putting small loops of variously colored thread through holes made near the edge of the mantle. In other animals, following the suggestion of G. Robilliard (personal communication) the dorsum was gently scraped to remove mucus, and spots of vital stains (*e. g.*, methylene blue) were applied. Finally, a method proposed by Dr. John Pearse was used. Using a fine scissors, a small V-shaped notch of tissue, approximately 1 mm across, was cut from the edge of the mantle. Notches could be made at 7 different locations. anteriorly, posteriorly, and centrally along both the left and right sides of the body and at the posterior end of the body. Because of the proximity of the oral tentacles, no notches were made at the anterior end of the body. Using combinations of one and two notches, many nudibranchs could be marked distinctively. The notches were detectable by careful examination of the edge of the mantle.

Unmarked animals were used as controls and were carefully chosen to be distinctive with respect to their coloration, size, and the pattern of the dark spots on the dorsal surface.

RESULTS and DISCUSSION

The first two marking techniques were not successful. Inserting a loop of thread into the mantle of *Rostanga pulchra* frequently tears the mantle. Once in place, the loops commonly snag and are torn out. In the case of marking with vital stains, some of the marks made were not easily visible and there was a high mortality rate among marked nudibranchs.

The reasons for this high mortality rate were not investigated. South's (1965) results suggest that vital stains are not toxic. However, scraping the dorsum may have caused injury and infection of the epithelium.

The notching technique was successfully used. The survival of notched *Rostanga pulchra* was first observed in the laboratory. Five marked and 5 control animals were kept in an aquarium with the sponge, *Ophlitaspongia pennata* Lambe, for food. The behavior of the nudibranchs and the condition of their wounds were observed daily. The observations were discontinued after 24 days due to the degeneration of the food sponge. The loco-

motory behavior of the notched animals did not differ from that of the controls. Both groups exhibited normal feeding and reproductive behavior. At the end of the observation period, 3 of the marked and 3 of the control animals were still alive. Two marked animals and one of the controls died from injuries received from the water pump of the aquarium. The other control animal died of unknown causes. Thus, under these aquarium conditions it appeared that the marking procedure did not affect the ability of the nudibranchs to survive. The notches were still easily detectable at the end of these observations.

A field experiment was then conducted with 8 pairs of nudibranchs. An attempt was made to choose as one member of each pair an animal that was sufficiently distinctive to be identified without being marked. This was not entirely successful. The other member of each pair was marked. As is apparent from the recovery data (Table 1), it is not always possible to identify unmarked animals with certainty. However, the recovery of marked *Rostanga pulchra* was similar to that of unmarked animals indicating that the marking method does not bias recovery.

Table 1

Results of a Marking Experiment

Four sites were chosen at each of which one or more pairs of *Rostanga pulchra* were found. One member of each pair, which was distinctive in appearance, was not marked. The other member of each pair was marked.

Site		Number of animals	Number of animals recovered on – days after marking: Day 1	Day 2	Day 3	Day 4
1	Marked	4	4	3	4	3
	Unmarked	4	5	4	4	3
2	Marked	1	1	1	1	1
	Unmarked	1	1	1	1	1
3	Marked	2	2	2	2	2
	Unmarked	2	2 (2)[1]	3 (1)	4	4 (3)
4	Marked	1	1	1	1	1
	Unmarked	1	1	1	0	1

[1] The animals listed in parentheses are unmarked animals, not fitting the descriptions of the original unmarked animals that were observed at the recovery sites.

According to SOUTHWOOD (1966) an effective marking technique should be durable, inconspicuous, and not affect the behavior or the longevity of the animals. Notching the edge of the mantle of *Rostanga pulchra* satisfies all of these criteria. Furthermore, nudibranchs can be notched quickly either in the field or in the laboratory. The technique is suitable for both group marking, in which large numbers of nudibranchs are marked identically, and for individually marking animals.

This marking method was used in extensive field observations (ANDERSON, 1972) to study the day to day movements of *Rostanga pulchra* within the intertidal zone. Nudibranchs ranging in length from 6 to 18 mm were successfully marked. Notched nudibranchs were recovered from the substrates on which they were initially found, as well as up to 60 cm away from their original locations. Twenty-nine animals were marked in one experiment; 24 of these animals (83%) were recovered on the first day after marking, 15 animals (52%) on the second and third days, and 11 animals (38%) on the fourth day. In one case a nudibranch was recovered 37 days after marking although this is not regarded as an upper limit. These experiments suggest that notching the edge of the mantle is an effective technique for marking dorid nudibranchs. It may also be useful for marking other mollusks.

ACKNOWLEDGMENTS

This work was done at Hopkins Marine Station of Stanford University and at the University of California, Berkeley. I thank Drs. Welton Lee and John Pearse for their many helpful suggestions during the course of the research.

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1971. The association of the nudibranch *Rostanga pulchra* MacFarland (1905) with the sponges *Ophlitaspongia pennata, Esperiopsis originalis,* and *Plocamia karykina.* Ph. D. thesis, Univ. Calif. Santa Cruz
in prep. Behavioral and ecological aspects of the association between *Rostanga pulchra* (Gastropoda: Nudibranchia) and the sponges *Ophlitaspongia pennata, Esperiopsis originalis,* and *Plocamia karykina* (Porifera: Demospongia).

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BOOKS, PERIODICALS, PAMPHLETS

Die miozäne Molluskenfauna
von Miste-Winterswijk NL (Hemmoor)

by Fritz Nordsieck. vi+188 pages, 3 text figures; 9 tables and over 350 drawings on 33 plates. Full linen, DM 118.- February 9, 1973.

A total of 337 species and subspecies are discussed. These include about 30 species and a dozen subspecies new to science. Many of the taxa discussed include minute shells, but all are well illustrated by pen-and-ink drawings by the author.

The material on which this book is based, consists of 5 kg of sieved material from various depths of a relatively new cut in Holland. To say that the material comes from various depths may convey a wrong picture, unless it is stated that the entire deposit is only 2½ m thick.

We believe that this book will be of interest to serious students of the Recent European marine molluscan fauna and is another in a valuable series of books published by Gustav Fischer in Stuttgart.

RS

Die Europäischen Meeresschnecken
(Opisthobranchia mit Pyramidellidae; Rissoacea)
Vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer.

by Fritz Nordsieck. xiv+327 pages; 1100 pen-and-ink drawings on 37 plates; 63 colored figures on 4 plates. Full linen, DM 74.-. November 8, 1972.

This is the third volume by the same author, dealing with various groups of molluscan orders from the same area. As its predecessors, this book is suitable for a study of the species of the groups mentioned in the title. A revision of the Rissoacea (including 320 species) forms an important part of the book.

There are about 100 new taxa (we counted 1 new family, 7 new subfamilies, 7 new genera, 26 new subgenera, 28 new species, 33 new subspecies, 18 new names and 34 new "forms" [these are not included in the count]). The author informed us in correspondence that he did not intend his "forms" to indicate anything more than the variability of the species concerned.

The descriptions of the various species, new and old, are clear and precise, and thus of great help to the serious student of the molluscan fauna of the European seas; they will also be of great use for comparative purposes in the study of related species from other sources.

When one considers the relatively short span of time in which the Gustav Fischer Verlag in Stuttgart was able to produce the entire series, one becomes aware that the author must have spent many years in the careful preparation of the text and the drawings.

RS

Malacological Review

P. O. Box 801, Whitmore Lake, Michigan 48189, U. S. A.
vol. 6, part 1: 103 pages, illustrated. 1973

As in the previous volume of this valuable publication, there are abstracts of the "Mollusk Seminar, Ann Arbor, 1972", as well as several original papers. An obituary with a portrait of the Australian malacologist Tom Iredale is included. Of special interest to many workers will be the historical sketch of the first 10 years of existence of the important journal Malacologia. In the "News" section is a detailed account of the formation of the Council of Systematic Malacologists. An excellent review of a recent Texas publication precedes the section on the Contents of Current Malacological Periodicals.

We cannot keep from commenting on the continued modest price of this publication, in spite of the ever increasing printing costs and postal fees, although some very slight adjustments have been made in the cases of foreign subscribers and those who must pay with UNESCO coupons. From our own experience along these lines, we must assume that the publisher absorbs a sizable deficit.

RS

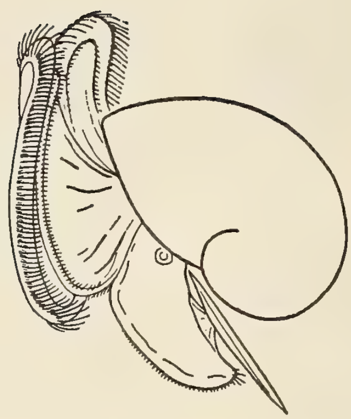
SHELLS in COLOR

A Studio Book. Photographs by Kjell Sandved; text by R. Tucker Abbott. 101 figures in full color on 64 plates; 8 text figures; 48 pages of text. $12.95. The Viking Press, New York, N. Y. 10022. April 27, 1973.

The illustrations in this comparatively small book are of superb artistic quality and carefully printed. The examples selected are some of the rarer species of molluscan shells and many of the "close-up" photographs are not only interesting from a purely esthetic point of view, but also of value to the sophisticated shell collector. The accompanying text by the well known malacologist, Dr. R. Tucker Abbott, however, makes it difficult to decide at

what market the book is aimed; it could not possibly be meant for foreign readers who must rely on their dictionaries for a complete understanding of the text, as they would fail to understand why a chapter heading states "Shells are living animals." Such purely vernacular use by the most unsophisticated beginning shell collector can be understood by the American reader. All of which leads us to believe that this book is intended to interest two groups of people, those who will enjoy the really superb pictures and those who may become interested in shells by glancing through this book. Fortunately, most of the text is written in a manner more up to the unquestionably solid malacological background of the author.

RS



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Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

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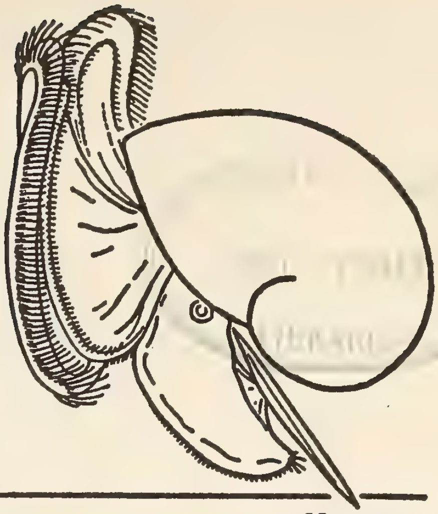

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ORDER, Suborder, **DIVISION**, **Subdivision**, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, *(Subgenus)*
New Taxa

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The "Juxtaganglionic" Tissue and the Brain of the Abalone *Haliotis rufescens* Swainson

BY

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(4 Plates)

INTRODUCTION

THE MOLLUSCAN JUXTAGANGLIONIC organ was first described by MARTOJA (1965a) in the opisthobranch gastropod *Hydromyles globulosa* (Rang, 1852), a planktonic gymnosome. This organ consists of tissue of glandular appearance in direct contact with each cerebral ganglion; it is well developed at the time of gonocyte maturation but begins to atrophy at fertilization. MARTOJA (1965b) reported on a similar structure in the opisthobranch *Aplysia punctata* Cuvier, 1804 and suggested on the basis of histochemical tests that it elaborated peptides. Subsequently she (1965c) described similar tissue in several diotocardian (archeogastropod) prosobranchs, notably *Diodora mamillata* (Risso, 1826), *Patella lusitanica* Gmelin, 1791, and *Trochocochlea turbinata* (Born, 1780), and called attention to the eosinophilic, granular character of the cytoplasm and the large nucleolus. She reaffirmed cyclic changes in appearance, namely, advanced development at the time of gonocyte maturation and atrophy at the time of gamete release.

We wish to provide the evidence for a similar tissue in the eastern North Pacific abalone, *Haliotis rufescens* Swainson, 1822, and to call attention to its proximity to possible neurosecretory regions in the cerebral ganglia. Inasmuch as this tissue has not been subjected hitherto to examination with the electron microscope, we also include some ultrastructural observations. Preliminary, successful attempts at organ culture of the cerebral ganglion-juxtaganglionic tissue complex are also described.

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MATERIALS AND METHODS

Red abalones, ranging from 16 to 26 mm in shell major diameter, were obtained by SCUBA diving at depths of 3 to 9 m, at Ocean Cove, Horseshoe Cove, and Bodega Rock in the vicinity of the University of California Bodega Marine Laboratory. They were used soon after capture or maintained in the aquaria of the laboratory. Cerebral ganglia with the apposed juxtaganglionic tissue, and pedal ganglia were fixed in either Stieve's solution or the Bouin-Hollande fluid. Paraffin sections were stained with hematoxylin and eosin, Heidenhain's azan, paraldehyde fuchsin, alcian blue, or Masson's trichrome.

For ultrastructural studies the cerebral and pedal ganglia were fixed in veronal acetate-buffered osmium tetroxide with added sucrose (300mg/ml) or paraformaldehyde/glutaraldehyde buffered with cacodylate to pH 7.5 (KARNOVSKY, 1965). The sections were stained with uranyl acetate and lead citrate prior to study in a Siemens Elmskop 1.

The intact cerebral ganglion, the ganglion with most of the juxtaganglionic tissue removed, juxtaganglionic tissue alone, and juxtaganglionic tissue plus the ganglion from which it was removed, were placed in organ culture. Several protein-augmented invertebrate culture media including Streiff's A6 without gelatin (STREIFF & PEYRE, 1963), Sengel's enriched marine invertebrate nutrient medium (ZILLER-SENGEL, 1970) and Streiff's A6 medium with abalone hemolymph substituted for the egg albumin were used, in addition to lyophilized medium 199 plus sea water.

An antibiotic mixture of penicillin (100 units/ml), streptomycin (100 μg/ml) and fungizone (0.25 μg/ml)

(Gibco) was added to all media. Cultures were incubated at 15° C and aerated with 95% O_2 - 5% CO_2. The media were changed every third day, and cultures were maintained for either 3 and 6 days, or 5 and 10 days.

OBSERVATIONS

Cerebral Ganglia

The neuronal perikarya are distributed at the periphery of the cerebral ganglia in the diffuse pattern characteristic of archeogastropods. The cytoplasm of the majority of neurons is uniformly stained by the counterstains of the methods used. A small number (less than 10%) of the neurons are lightly stained peripherally with paraldehyde fuchsin. In addition, there are some structures about the size of neurons, also located in the neuronal zone, that are strongly stained with paraldehyde fuchsin. These structures appear to be clumped masses of "blood cells" in sections that are stained by azan and Masson's trichrome.

The bulk of the ganglion is composed of neuropil. Concentrations of axons containing the possible neurosecretory material are present immediately below the thin layer of neurons. This concentration of paraldehyde fuchsin-stained fibers is especially rich in the dorsal region of the ganglion near the base of the cerebropleural connective (Figures *1* - *3*). Stainable axons in this region were consistently noted in all animals examined and did not appear to vary substantially with seasonal or physiological (spawning) changes. Attempts to trace the stained axons either to stained cell bodies or to neurohemal areas were unsuccessful.

Ultrastructurally, most cerebral neurons contained the usual cytoplasmic organelles along with large membrane-bound inclusions showing various degrees of internal organization (*cf.* SIMPSON *et al.*, 1966). The nature of the inclusions varied: Some were composed of packed membranes or filaments; others were composed of clumps of strongly osmiophilic material or of homogeneous pale material; frequently a single inclusion showed all 3 features. Other neurons, fewer in number, contained small dense granules similar in appearance to typical elementary neurosecretory granules, in addition to the large inclusions (Figure *4*).

Many axons in the neuropil adjacent to the neuronal layer contained elementary granules as well as vesicles of various sizes (Figure *5*). The paraldehyde fuchsin- and alcian blue-staining region of the neuropil presumably represents this layer of granule-containing axons (Figures *2*, *3*). In addition, there were a few processes bearing neurosecretory-like granules in the loose connective tissue enveloping the cerebral ganglion (Figure *6*). These axon-like processes were too few in number to be detectable with the light microscope.

Explanation of Figures *1* to *4*

Figure *1*: Wholemount of right cerebral ganglion of *Haliotis rufescens*. Circled area is at dorsal side of ganglion, where cerebropleural connective (CPL) joins and where juxtaganglionic tissue is particularly concentrated. Concentrations of this tissue are also found at bases of optic nerve (ON) and tentacular nerve (TN). Also shown are the cerebropedal connective (CPD) and the cerebral commissures (CC). Haematoxylin and eosin. × 10

Figure *2*: Left cerebral ganglion (CG) of *Haliotis rufescens* in frontal section, just dorsal to junction with cerebropleural connective (CPL). Mature animal (major shell diameter 170 mm). Note possible neurosecretory material (NSM). Paraldehyde-fuchsin. × 100

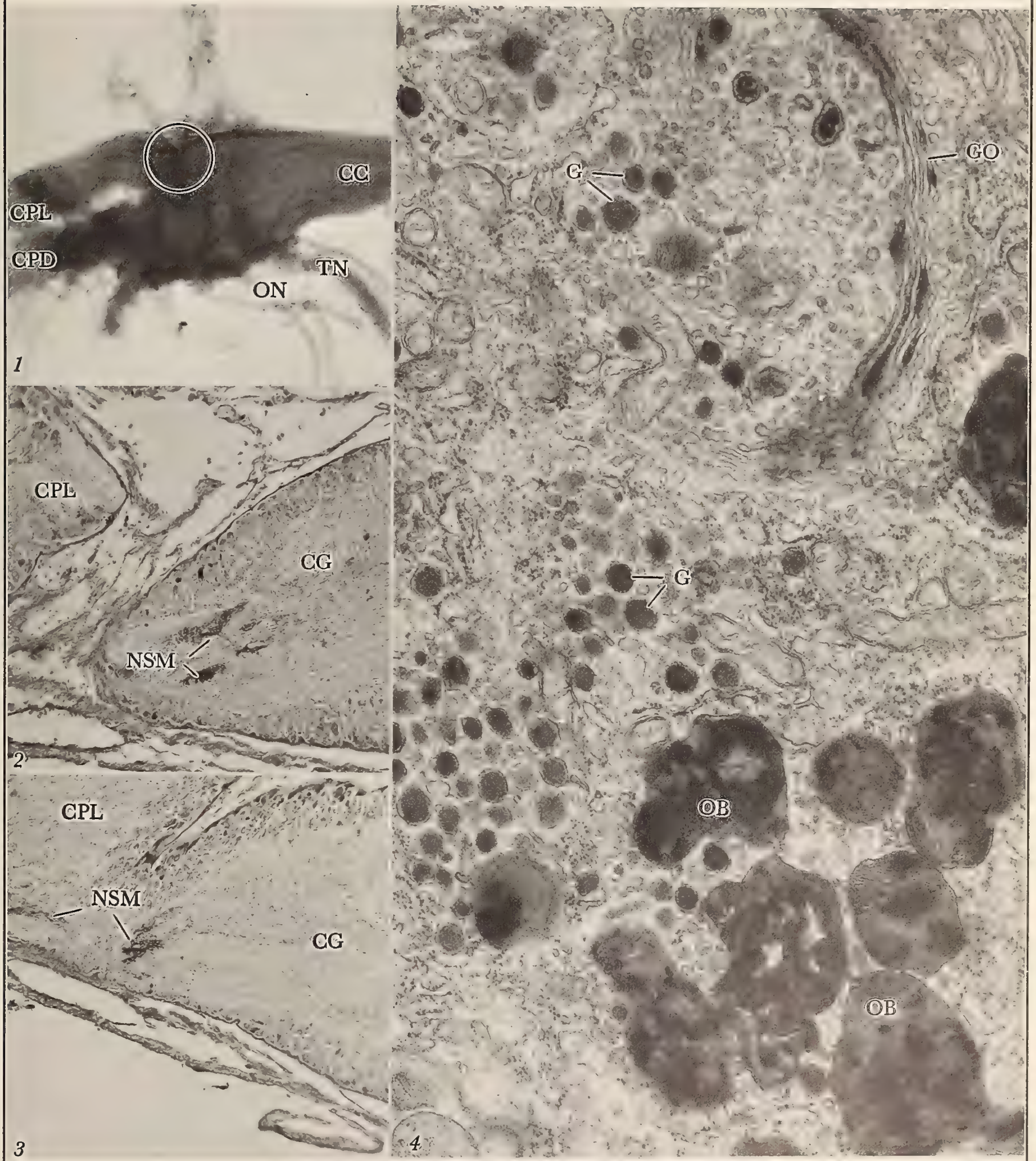
Figure *3*: Same as Figure 2, but more ventral, at junction of cerebropleural connective (CPL) and cerebral ganglion (CG). Possible neurosecretory material (NSM). × 100

Figure *4*: Electron micrograph of portion of neuron from cerebral ganglion containing elementary granules (G) and larger osmiophilic bodies (OB) composed of lamellae, fine fibrils and amorphous structures of varying electron density. Golgi systems (GO) appear very active. × 30 000

Explanation of Figures *5*, *6*

Figure *5*: Electron micrograph of portion of neuropil adjacent to neuronal layer of cerebral ganglion. Note part of one axon with electron-dense granules (G) and irregular vesicles and other axons with small vesicles. Part of another axon contains large granulated vesicles (LGV). Polystyrene spheres = 264 nm. × 30 000

Figure *6*: Electron micrograph of periphery of mitochondria-rich cell of juxtaganglionic tissue with vesiculated osmiophilic bodies (VB) as well as homogeneous inclusions (I). A granule filled process – presumably an axon (A) – lies adjacent to it. × 10 000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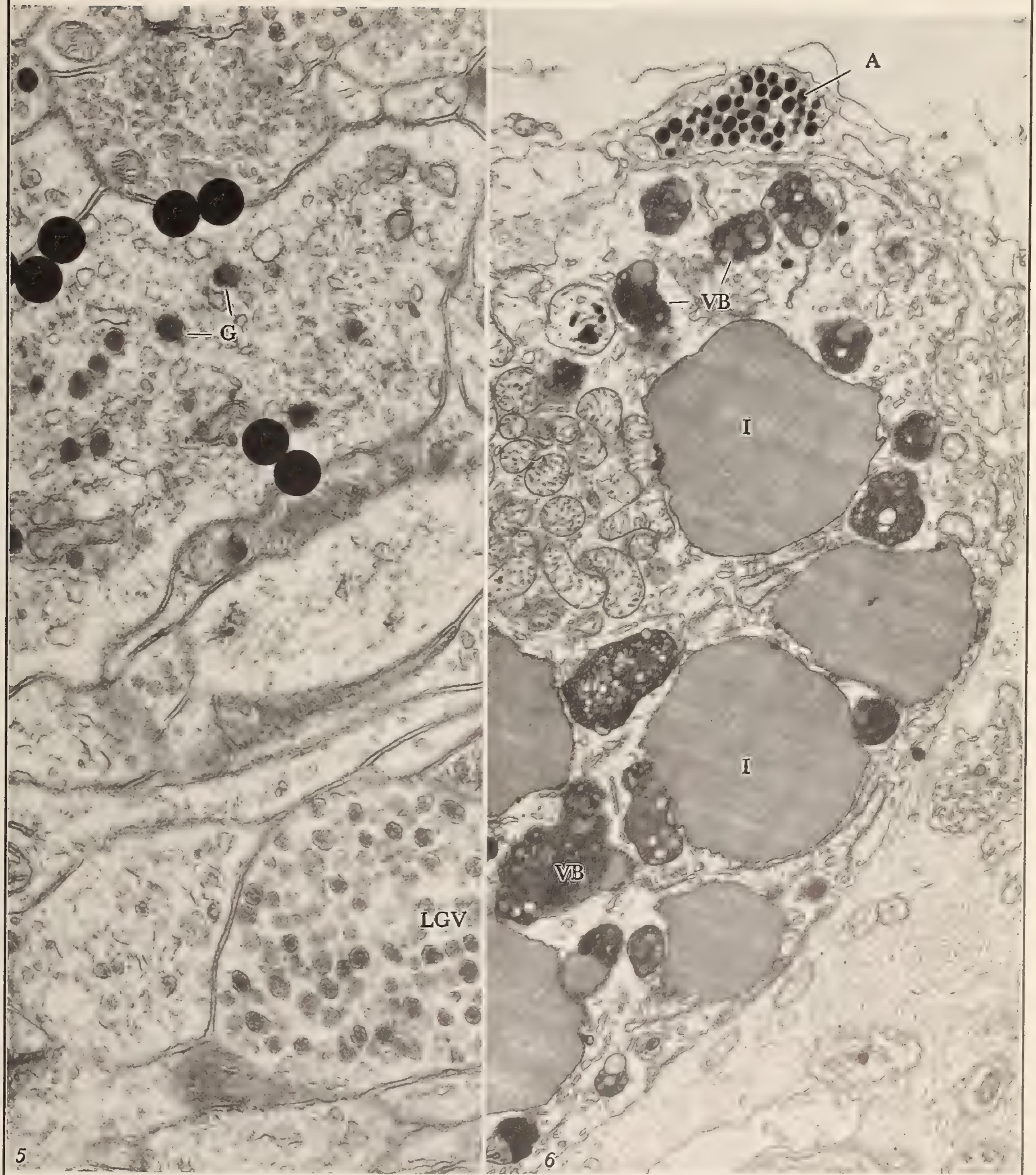
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Juxtaganglionic Tissue

The large cells that constitute the juxtaganglionic tissue of the abalone lie in the connective tissue surrounding the cerebral ganglia (Figure *7*). In young and juvenile abalones (major shell diameter 2 cm to 9 cm) the cytoplasm of the large juxtaganglionic cells appears finely granular and stains with acidophilic dyes; the cells are situated dorsally above the base of the cerebropleural connective. In the larger juveniles, some of the juxtaganglionic cells are also present in a more ventral location. The juxtaganglionic cells of the mature abalones (major shell diameter 10 cm to 26 cm) prior to spawning are very large and contain an acidophilic, finely granular cytoplasm. The large nucleus contains a prominent nucleolus. The greatest concentration of juxtaganglionic cells occurs at the base of the cerebropleural connective, but the cells are spread over the bases of the optic and tentacular nerves as well (Figure *8*). Animals with mature-appearing gonads possess more juxtaganglionic cells (Table 1). In animals sacrificed immediately after induced spawning, shrinkage of the cytoplasm of the juxtaganglionic cells was noted (Figure *9*).

Table 1

Numbers of Abalone showing Juxtaganglionic Cells with Finely Granular (Mitochondria-rich?) Cytoplasm at Different Times of the Year

Months	No. of Animals Studied	No. (%) with Granular Cells
February - May	11	11 (100%)
August - September	9	8 (90%)
October - November	9	3 (33%)

Another type of large cell was found in the connective tissue both of the cerebral ganglion (Figure *8*) and of the pedal ganglion (Figures *11* and *12*). This type of cell contained large refractile granules and a small nucleus without a prominent nucleolus. These cells were found in varying numbers in most adults examined but were absent from the few immature specimens studied. It is uncertain whether the characteristic orange-brown pigmentation seen *in vivo* on the surface of the cerebral ganglion is attributable to the juxtaganglionic tissue or to the refractile granule-laden cells.

Most of the animals providing tissues for electron microscopy were mature. Large cells which contained a prominent nucleolus and many small mitochondria are presumed to correspond to the acidophilic, finely granular cells of light microscopy. The mitochondria occupy up to one-third of the cytoplasmic area of these cells. The mitochondria-rich cells also contain some large vesiculated osmiophilic bodies and some homogeneous inclusions, possibly lipid in nature, at their periphery (Figures *6* and *10*). Mitochondria-rich cells are fewer in number in abalones taken in October and November. The second type of large cell associated with the juxtaganglionic tissue and with the connective tissue of the pedal ganglion (Figures *11* and *12*) also contains many large homogeneous inclusions (refractile granules) some of which are similar to those found in mitochondria-rich cells (Figure *6*). However, the nuclei of these latter cells are relatively small and dense and lack nucleoli. No synaptic contacts of granule-containing axon-like processes with juxtaganglionic cells were seen, although some processes were in close proximity to the cells (Figure *6*).

In Vitro Culture Experiments

Four different media were used initially in the 3- and 6-day organ cultures. Medium 199 plus sea water allowed the best maintenance; therefore, it was used subsequently for the 5- and 10-day cultures. In the intact cerebral ganglion-juxtaganglionic tissue complex, only a few pycnotic nuclei were observed in the connective tissue sheath after 5 days (Figure *13*). The neurons all appeared normal except near the severed connectives. The juxtaganglionic cells with acidophilic, finely granular cytoplasm (mitochondria-rich cells), as well as the refractile granule-bearing cells, seemed unchanged. Even after 10 days the intact cerebral ganglion complex was well maintained except for the occurrence of many more pycnotic nuclei in the connective tissue sheath (Figure *14*).

The cerebral ganglion with much of the juxtaganglionic tissue removed showed considerably more pycnotic nuclei in the connective tissue sheath as well as in the neuronal layer, even after only 5 days in culture. The juxtaganglionic tissue alone survived poorly, and most of the cells were condensed and appeared moribund after 5 days *in vitro*; however, juxtaganglionic tissue co-cultured with nervous tissue showed some peripheral cells which appeared normal.

DISCUSSION

Martoja (1965a, b, c) reported juxtaganglionic tissue on the dorsal surface of the cerebral ganglia in several opisthobranchs and archeogastropods; in the archeogastropod *Patella lusitanica,* this tissue was located laterally around the base of the optic nerve, rather than dorsally.

In *Haliotis rufescens,* the presumably equivalent tissue occurs dorsally and laterally, as well as medially (on the inner face of the ganglion). It is generally distributed diffusely within the connective tissue immediately adjacent to the ganglion, but it is particularly concentrated above the root of the cerebropleural connective and at the bases of the optic and tentacular nerves.

A glandular nature of this tissue is suggested by its histological appearance. In very young animals the cells are small and rounded and can be distinguished from connective tissue cells and hemocytes by their large, round nucleus with prominent nucleolus; in mature animals, the cells are very large, with acidophilic, finely granular cytoplasm and a very prominent nucleolus. No ductal structures were seen, suggesting a possibly endocrine function.

Ultrastructurally, the mitochondria-rich cells are considered to be the juxtaganglionic tissue proper, and the homogeneous inclusion-laden cells are viewed as connective tissue or hemal elements, not confined to the cerebral ganglion inasmuch as similar cells were also found in the connective tissue of the pedal ganglion. It is possible that some of the homogeneous inclusion-laden cells may be derived from the mitochondria-rich cells; some osmiophilic bodies were encountered at the periphery of the latter.

The Japanese abalone, *Haliotis discus hannai* Ino, 1953, breeds between August to October (Yahata & Takano, 1970). *Haliotis rufescens* was observed spawning in the laboratory in late fall. This correlates well with the decline in the number of juxtaganglionic cells in October and November. This decline may start earlier but may not be very noticeable, because *H. rufescens* apparently spawns only partially at any one time.

A suggestive finding is the proximity of possible neurosecretion in a plexus within the cerebral ganglion. Although no neurohemal organ was found, neurohormone could be released at some point into the hemolymph, inasmuch as neurohemal areas at the surface of ganglia, connectives and nerves are very common in at least some gastropod species (*cf.* Bonga, 1970). The adjacent juxtaganglionic tissue, itself bathed in hemolymph, would provide a possible target organ.

The juxtaganglionic tissue can be classified as a kind of "dorsal body", such as is found in pulmonate gastropods. Indeed, as Joosse (1972) points out, these structures are likely to be homologous among the gastropods. The indeterminate relationship of the juxtaganglionic cells to the cerebral ganglion resembles that seen between the (medio)dorsal body and the cerebral ganglion in pulmonates (*cf.* Boer *et al.*, 1968); Simpson, 1969), except that the dorsal body cells give rise to a network of granule-laden processes apposed to the ganglionic surface, which is not evident in the abalone tissue. The *Haliotis* juxtaganglionic cells are not so conspicuously secretory as is claimed by Vicente (1970) and Vicente & Gasquet (1970) for the cells of the juxtacommissural organ, presumably equivalent to the gastropod cells, of two species of chiton.

The cerebral ganglion with its associated juxtaganglionic cells survives remarkably well in organ culture. However, the connective tissue sheath containing juxtaganglionic cells alone degenerates in culture. Some damage no

Explanation of Figures *7* to *10*

Figure *7*: Left cerebral ganglion of immature *Haliotis rufescens* (major shell diameter 25 mm); frontal section at junction of cerebbropleural connective (CPL) with cerebral ganglion (CG). Note juxtaganglionic cells (JG). Haematoxylin and Eosin. × 400

Figure *8*: Right cerebral ganglion of maturing *Haliotis rufescens* section near junction of cerebropleural connective with cerebral ganglion (CG). Juxtaganglionic cells (JG) contain cytoplasmic masses and prominent nucleoli. Note other granular cells (GC) in connective tissue. Masson's. × 400

Figure *9*: Juxtaganglionic tissue (JG) in mature *Haliotis rufescens* (major shell diameter 128 mm) shortly after spawning. Note reduced size. Right cerebral ganglion (CG). Azan. × 400

Figure *10*: Electron micrograph of mitochondria-rich cell from juxtaganglionic tissue region with large vesiculated osmiophilic bodies (VB) as well as other inclusion bodies with areas of varying osmiophilia. × 10 000

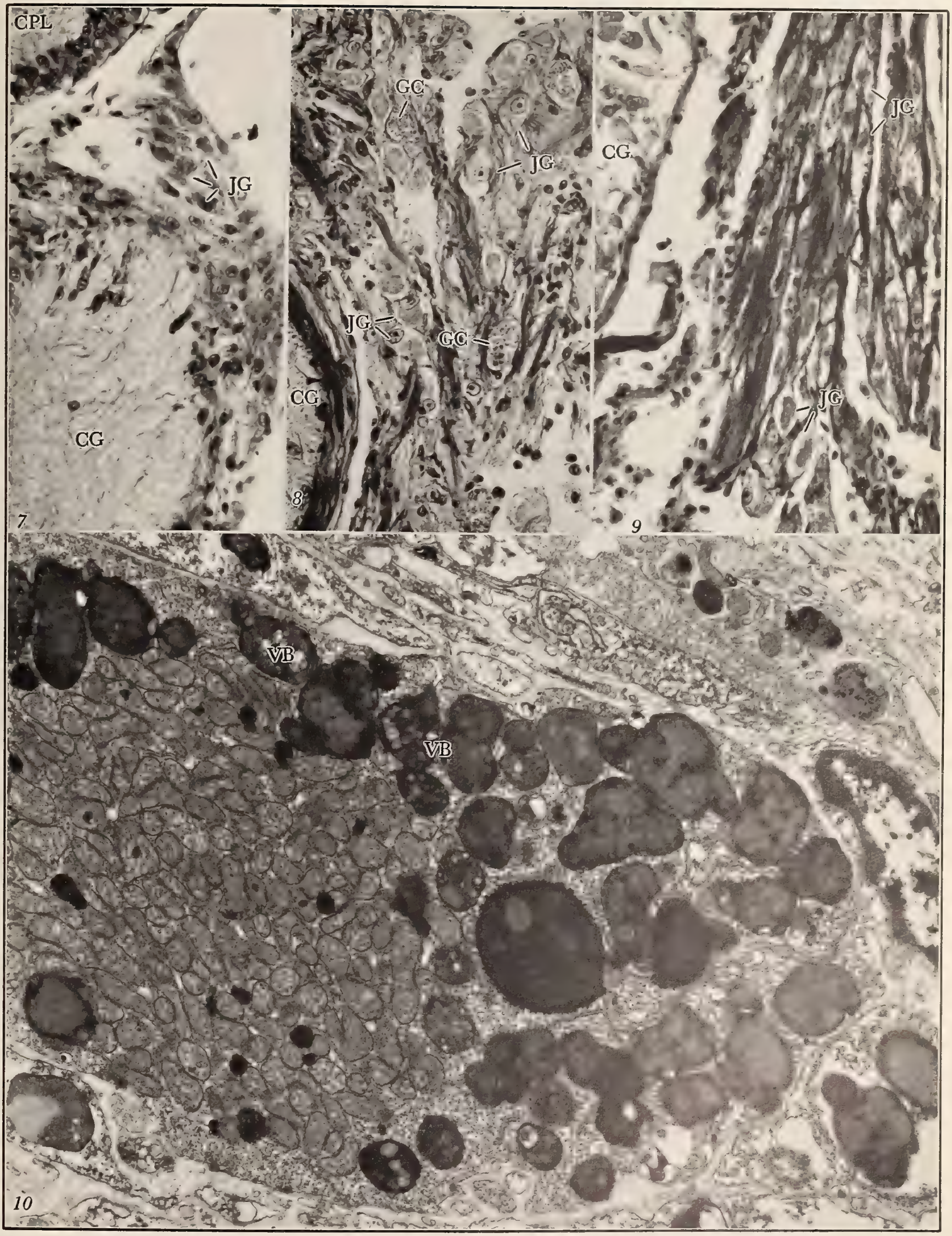
Explanation of Figures *11* to *14*

Figure *11*: Section of pedal ganglion (PG) and adjacent connective tissue. Note cells with large granules (GC). Masson's. × 400

Figure *12*: Electron micrograph of portion of cell with large homogeneous inclusions from connective tissue of pedal ganglion. Compare with homogeneous inclusions found in mitochondria-rich cell (Figure *6*). × 5 000

Figure *13*: Portion of intact cerebral ganglion-juxtaganglionic tissue cultured in medium 199 plus sea water for 5 days. Few pycnotic nuclei present. Compare with Figures 7 and 8. Masson's. × 400

Figure *14*: Portion of intact cerebral-juxtaganglionic tissue cultured in medium 199 plus sea water for 10 days. Some evidence of tissue breakdown can be seen in both cerebral ganglion and connective tissue. Connective tissue capsule surrounding cerebral ganglion has undergone partial degeneration. Compare with Figures *7* and *8*. Masson's. × 400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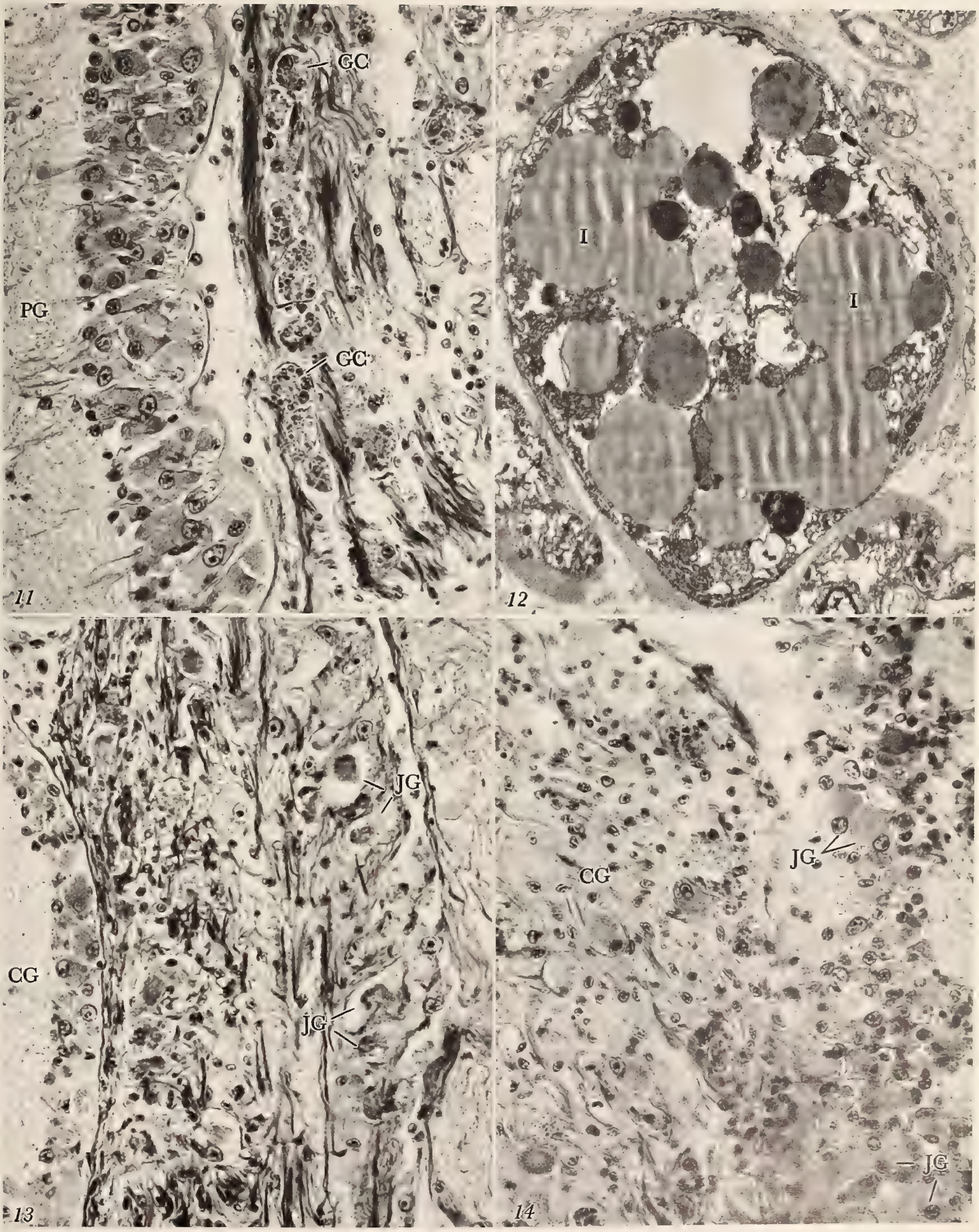
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doubt takes place when the sheath is stripped away from the ganglion; this may also account for the poor survival of parts of the isolated ganglion. In cultures where the separated sheath containing juxtaganglionic cells was placed adjacent to the ganglion, some of the juxtaganglionic cells at the periphery of the sheath appeared normal. Thus, there is some evidence for occurrence of a tropic factor (neurohormone?) elaborated by the nervous tissue, which contributes to the survival of the juxtaganglionic cells.

ACKNOWLEDGMENTS

We wish to express our gratitude to Dr. Fred Clogston of the California Polytechnic University at San Luis Obispo for his advice on the care and feeding of abalones and his references to pertinent literature; to Mrs. Anne Mos and Dr. Jacqueline Naisse for their assistance and recommendations in regard to histological techniques; to Mrs. Shirley Sanderson for advice and assistance with organ culture, and to John Underhill for his photographic assistance. Thanks are also due the staff of the Bodega Marine Laboratory for their hospitality and help, and Lloyd Austin, Jerry Tinkess, Bill Splaine, Tim Hollibaugh and Dave Zittin who assisted in procuring animals. This work was aided by NIH postdoctoral fellowship No. 1 FO2 GM41120-01 to Walter Miller and by NSF grants GB-6424 and GB-23033.

SUMMARY

The cerebral ganglion and its associated juxtaganglionic tissue was studied in the red abalone, *Haliotis rufescens*, by light and electron microscopy. Most of the neurons contained large inclusion bodies, and a few neurons also contained small dense granules resembling elementary neurosecretory granules. Below the peripherally located neuronal zone was a layer of axons which stained with paraldehyde-fuchsin and contained elementary granules. In the connective tissue sheath adjacent to the neuronal layer were found mitochondria-rich cells (juxtaganglionic tissue) and other inclusion-bearing cells. Organ cultures of the cerebral ganglion-juxtaganglionic tissue complex survived well for more than a week *in vitro* but either tissue alone did not survive so well. Co-culture of the separated juxtaganglionic tissue with the ganglion led to somewhat improved maintenance of the former.

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The Northwest American Donacidae

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(1 Plate; 2 Text figures)

INTRODUCTION

THIS IS THE FOURTH ARTICLE based on research conducted while I was a graduate student at Stanford University, the Tellinidae, Semelidae, and Psammobiidae having been discussed in earlier papers (COAN, 1971, 1973a, 1973b). The main purpose of the present account is to put on record data on the systematics of the northwest American Donacidae, those occurring from arctic Alaska to the central portion of the outer coast of Baja California. The present survey also permitted the review of data on the geographic and geologic distributions and habitats of this family. These aspects are summarized at the end of this article.

The major previous accounts on this family in northwestern America were those of STRONG (1924), GRANT & GALE (1931), and BURCH (1945a-1945b). MORRISON (1971) has recently discussed the western Atlantic species.

The detailed "Introduction," "Acknowledgments," and "Methods" sections of my earlier paper on the Tellinidae (COAN, 1971) need not be repeated here, although special thanks are extended to Drs. A. Myra Keen, Warren O. Addicott, and Kenneth J. Boss who reviewed the present manuscript, and to Mr. Barry Roth who prepared the illustrations. The following abridged comments on format and abbreviations will permit the present paper to stand alone.

(1) The applicable synonymous species-level names are listed in chronological order, with the name to be used cited first and "first revisions," if any, indicated. Under each name are listed accounts published using those names and also accounts of type material pertinent to each. These works are listed in chronological order.

The works listed do not represent a complete catalogue of literature but are the major accounts concerning living and fossil northwest American material, particularly those containing previously unpublished information or taxonomic innovations. Not included are books written largely for amateurs or general works on marine biology.

Numbers following dates (as 1851: 27) are page numbers.

(2) The type material pertinent to the valid name and its synonyms is discussed. Measurements given are of the greatest lengths of type specimens. When type material is no longer extant the dimensions from original accounts or of original illustrations are given. (In most early accounts the illustrations were usually printed at natural size, though this was rarely stated.) Photographs of type specimens or of original illustrations are included.

(3) Type localities of the various nominal species are given. The original collector is also cited.

(4) A nomenclatural commentary may be given to explain nomenclatural complications not made clear in the synonymy or in the discussion of type material.

(5) Description. A short diagnosis of each species is given that emphasizes distinguishing characters. Most features of internal shell morphology are not discussed in detail but are illustrated with line drawings.

(6) Geographic Distribution and Ecology. The end-points of the distribution are given, together with reference to the sources of the records. The intermediate distributional data from between these end-points are summarized.

The sources of habitat information on each species other than from museum labels are indicated. I mention also the approximate number of lots examined.

(7) Geologic Distribution and Biogeography. The final section under each species is a summary of paleontologic records from published accounts. I have not listed all Pleistocene records, but generally have given only the end-points of their distributions and indicated the published accounts that form their bases. This is followed by

notes on earlier records, on what seem to be related west American fossil species from earlier than the Pleistocene and other related species in other provinces.

References are included under "Literature Cited" for all genera, species, and papers mentioned.

Conventions, symbols, and abbreviations used are as follows:

AMNH – American Museum of Natural History, New York, New York
ANSP – Academy of Natural Sciences, Philadelphia, Pennsylvania
Berry Collection – The private collection of Dr. S. Stillman Berry, Redlands, California.
BM(NH) – British Museum (Natural History), London, England
CAS – California Academy of Sciences, San Francisco, California
ex (Conrad) MS – from the manuscript name of (Conrad)
ICZN – International Commission on Zoological Nomenclature, or International Code of Zoological Nomenclature
"in synonymy" – a name proposed in the synonymy of another and therefore not available
m – meter(s)
MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
mm – millimeter(s)
not, not of – as in the case of homonyms or misidentifications
pair – the two valves of one specimen
SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, California
SDNHM – San Diego Natural History Museum, San Diego, California
SU – Stanford University, Stanford, California
UCB – University of California at Berkeley, California
UCD – University of California at Davis, California
USNM – United States National Museum, Smithsonian Institution, Washington, District of Columbia

SYSTEMATIC ACCOUNT

Donacidae Fleming, 1828

Within the Tellinacea, the Donacidae and the Psammobiidae retain characters that I regard as being more primitive than either the Tellinidae or the Semelidae, although they retain somewhat different sets of such features.

There are many published studies on the anatomy and functional morphology of members of this family. Most of these are not concerned with west American species and are not reviewed in detail. However, key papers are White (1942), Yonge (1949) (who reviews other earlier papers), Purchon (1960), Stasek (1963), Trueman (1966), Pohlo (1967), and Jegla & Greenberg (1968).

The Donacidae may be defined as those Tellinacea that are relatively trigonal, equivalve, and that lack either a posterior flexure or a gape. The ligament is entirely external but not seated on a conspicuous nymph. There are 2 cardinal teeth in each valve and well-developed lateral teeth in the left valve, with corresponding sockets and sometimes lateral teeth in the right valve. The siphons are short and stout.

Donax Linnaeus, 1758

[Type species: *Donax rugosus* Linnaeus, 1758; by subsequent designation of Schumacher, 1817]

Radial sculpture predominates in the genus *Donax*, often present only as marginal crenulations. Attempts to subdivide the species of *Donax* into subgenera described to date prove unsatisfactory, a conclusion reached previously by Keen (1971).

Hertlein & Grant (1972) suggest *Serrula* Mörch, 1853, *ex* Chemnitz MS, for *Donax gouldii*, but the species upon which it was based, *D. trunculus* Linnaeus, 1758 (by the subsequent designation of Stoliczka, 1870), is somewhat inflated anteriorly, smooth within posteriorly, and is said to lack lateral teeth in the right valve (Keen, 1969).

Paradonax Cossmann, *in* Cossmann & Peyrot, 1911 (type species: *Donax transversus* Deshayes, 1830, by original designation) might be used as a subgenus for *D. californicus*, although *D. transversus*, unlike *D. californicus*, is said to lack radial sculpture on the ends of the shell (Keen, 1969).

Donax gouldii Dall, 1921

(Figures 1 to 3 and 7)

Donax gouldii Dall [*gouldi*, of authors, misspelling]
Dall, 1921: 49 [not described in 1919, as stated]
Dall, 1923: 49
Strong, 1924: 83 - 84
I. Oldroyd, 1925: 183; plt. 49, figs. 8, 9
Grant & Gale, 1931: 380, 906; plt. 13, fig. 12
Burch, 1945a: 20 - 21, 24 - 26 (text figs.); 1945b: 17
Gregg, 1945: 20 - 21 [in the above]

Donax obesus Philippi, not of d'Orbigny, not of Gould
[not d'Orbigny, 1845: 54; 1847: plt. 81, figs. 28 - 30]
Philippi, 1851 (July): 75
[not Gould, 1851 (November): 90]

Donax obesus Gould, not of d'Orbigny, not of Philippi
[not d'Orbigny, 1845: 54; 1847: plt. 81, figs. 28 - 30]
[not Philippi, 1851 (July): 75]
Gould, 1851 (November): 90
Gould, 1853: 394 - 395, 408; plt. 15, fig. 9
Gould, 1862: 212
Johnson, 1964: 117

Donax laevigatus Reeve, *ex* Deshayes MS, not of Gmelin [as *D. "laevigata"*]
[not Gmelin, 1791: 3265]
Reeve, 1854: plt. 5, fig. 31
Deshayes, 1855: 352
Sowerby, 1866: 309; plt. 2, figs. 30 - 32
Bertin, 1881: 66, 91
Dall, 1900: 969
Arnold, 1903: 170 - 171, 388; plt. 13, fig. 8

Donax californicus Conrad, of authors, not of Conrad
[not Conrad, 1837: 254; plt. 19, fig. 21]
Gould & Carpenter, 1857: 200
Carpenter, 1857a: 213
Carpenter, 1857b: 195 - 196, 227, 229, 232, 241, 246, 287, 296, 304, 349, 351, 352
Carpenter, 1857c: 47, 548
Carpenter, 1864: 536, 540, 640, 665 [1872: 22, 26, 126, 151]
Römer, 1870: 41 - 43; plt. 4, figs. 5 - 8

Donax abruptus Carpenter, *ex* Gould MS [in synonymy]
Carpenter, 1857b: 232
Carpenter, 1864: 542 [1872: 28]

Type Material:

Donax gouldii – USNM 664935, holotype, pair, 23.2 mm. Dall's taxon was based on Gould's (1853) figures; thus the figured specimen is the holotype. Figure *1*.

Donax obesus Philippi – Lost, according to Drs. Kilias and Tembrock of the Zoologisches Museum, Humboldt Universität, Berlin (in correspondence), 20.7 mm (Philippi, 1851). The description is sufficient to place this taxon in synonymy.

Donax obesus Gould – USNM 664935, **lectotype** herein, pair, 23.2 mm; USNM 664936, **paralectotypes**, 5 pairs. Figure *1*.

Donax laevigatus – BM(NH), without registry number, **lectotype** herein, pair on extreme left on card, 23 mm; **paralectotypes**, 2 other pairs. Figure *2*.

Type Localities:

Donax gouldii and *D. obesus* Gould – San Diego, California; T. P. Green.

Donax obesus Philippi – California; "from a dealer."

Donax laevigatus – North America; Cuming collection (Deshayes, 1855).

Nomenclatural Commentary:

This common southern Californian species has suffered a complicated nomenclatural past.

Two names proposed for it have proved to be junior homonyms – *Donax obesus* (proposed twice, independently!) and *Donax laevigatus*. It was finally named *Donax gouldii* by Dall (1921), but Dall did not expressly propose his taxon as a replacement, so *Donax gouldii* must be regarded as a new species. As such, it is based on the specimen figured by Gould (1853), for Dall (1921) cited this figure. This specimen came to light in the course of the present study.

Nuttall evidently never correctly understood what it was from among his material Conrad had described as *Donax californica,* and he labeled the specimens of *D. gouldii* that he took to Europe (Figure *3*) as *D. californica.* This is the reason that Carpenter and others also became confused and used the name *D. californica* for the wrong species.

Gregg (1945), John Q. Burch (1945a) and Tom Burch, *in* John Burch (1945a), suggested that there are two distinct forms of this species which occur in "pure" colonies.

One form, the true *Donax gouldii,* was characterized by these authors as being short, rounded posteriorly, obese, and almost lacking in radial color rays. It is supposed to be more southern in distribution (San Diego, California, to Bahía Todos Santos, Baja California Norte).

The second, unnamed but still more common, was characterized as being more elongate, squarely pointed anteriorly, with conspicuous radial color rays. It is supposed to occur farther north in southern California (as at San Pedro) but also to occur as far south as Bahía Todos Santos.

Two illustrations accompany the text (first form, figure "MS 4411"; second, "MS 4410"), and Tom Burch *in* John Burch (1945a), said that these illustrate hinge differences not discussed in the text. It is difficult to detect any significant differences, but perhaps the first form is supposed to differ from the second in having a longer ligament, heavier laterals, and a less delimited posterior adductor muscle scar.

An examination of specimens in the California Academy of Sciences does not demonstrate any of these differences. For instance, some short, obese specimens (CAS 4878) have conspicuous radial rays. Hinge differences of the sort suggested are not apparent.

It is more likely that these differences represent character patterns associated with habitat. The short, obese form may be typical of populations on exposed beaches, while the more elongate form may represent those from semi-protected, bay entrance locations.

Description:

Medium-sized for genus (to 31.5 mm); ovate; inflated; relatively heavy; anterior end markedly longer, rounded; posterior end abruptly truncate; ventral edge evenly rounded to slightly flexed posterior to beaks; surface relatively smooth, shiny, but with obscure, underlying radial sculpture; periostracum thin, shiny; shell often rayed, banded, or blotched with brown, tan, blue, or other colors; interior ventral margin roughened by ends of radial sculpture. Other internal details as in Figure 7.

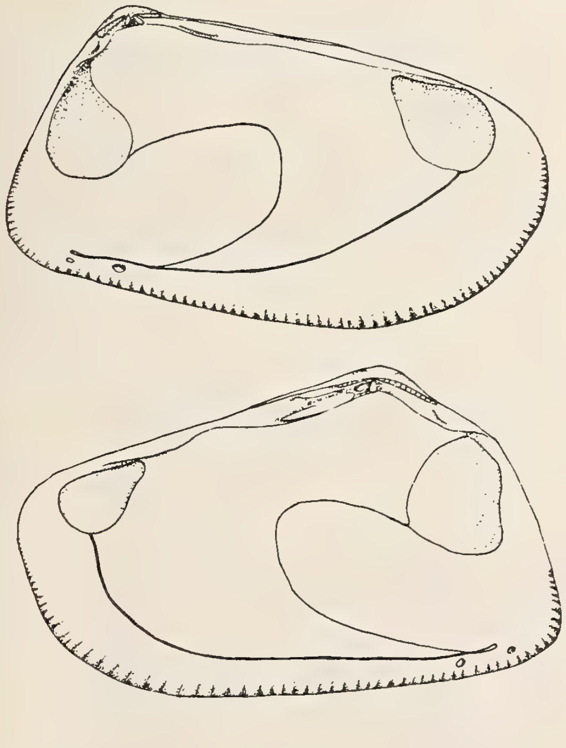

Figure 7

Donax gouldii

internal view of valves, SU 50, Long Beach, California

Geographic Distribution and Ecology:

Dillon Beach, Tomales Bay, California (Hedgpeth, *in* Marcus, 1961: 58); Davenport, California (collection of Mrs. Charles McLean); Monterey, California (MCZ 118780; AMNH 32896; ANSP 225910); San Luis Obispo-Pismo Beach area, California (UCD unnumbered; SDN HM 20042; SBMNH 10666) to Bahía Magdalena, Baja California Sur (USNM 41592; ANSP 52962; SDNHM 14976). Records from north of the San Luis Obispo area, California, probably represent larval settlement in particularly warm years. It is common between San Luis Obispo and Bahía Magdalena. Specimens in collections reportedly from Mazatlán, Sinaloa (SU 50/3), and from the Gulf of California (UCB 2404) probably represent labeling errors.

This filter feeding species occurs intertidally, but occasionally as deep as 5 m, in sand, mainly on open beaches, but also in semi-protected environments near bay entrances. The favored habitat is reported to be gently sloping beaches composed of firm, fine sand (Weymouth, 1921; Fitch, 1953; Coe, 1955; Johnson, 1966a, 1966b; Pohlo, 1967; Irwin, 1973).

Most individuals align themselves along the coast, broadside to the waves. Unlike other species of *Donax,* migration up and down the beach (as opposed to along) is minimal. Many specimens have colonies of the hydroid *Clytia bakeri* Torrey, 1904, attached to their posterior slopes.

This species occurs in very large numbers, sometimes as many as 20 000 to 32 000/m² (Coe, 1953, 1955; Pohlo, 1967). Population size fluctuates greatly from year to year, evidently caused in part by parasitic infections. Individuals can live up to 3 years, and spawning occurs from April to October or November (Coe, 1955). Internal morphology and behavior were discussed by Pohlo (1967), and Irwin (1973) treated several aspects of behavior.

Material seen:

221 lots.

Geologic Distribution and Biogeography:

Donax gouldii has been reported in the late Pleistocene from Santa Monica, California (Hoots, 1931; Valentine, 1956), to Bahía Magdalena, Baja California Sur (Jordan, 1936), with many intermediate records. In the early Pleistocene it is reported from the northern portion of the Los Angeles Basin (Rodda, 1957) and from the San Pedro area (Arnold, 1903; Clark, *in* Natland, 1957), California. This species is also known from formations transitional between the Pliocene and the Pleistocene (Arnold, 1903; Waterfall, 1929), and it has

recently been recorded from the Pliocene (HERTLEIN & GRANT, 1972). Its relationship to species reported from the west American Eocene to Miocene is unclear, as are its alliances to species living in the Panamic province or in Japan.

Donax californicus Conrad, 1837

(Figures *4*, *5*?, *6*, and 8)

Donax californicus Conrad, but not that of some authors [as *D. "californica"*]

CONRAD, 1837: 254; plt. 19, fig. 21
BERTIN, 1881: 66, 92
DALL, 1900: 968 - 969
ARNOLD, 1903: 170, 388; plt. 8, fig. 9
DALL, 1921: 49
DALL, 1923: 49
STRONG, 1924: 81 - 83
I. OLDROYD, 1925: 183
GRANT & GALE, 1931: 379 - 380
BURCH, 1945a: 20; 1945b: 17
HERTLEIN & STRONG, 1949: 252 - 253, 258; plt. 1, figs. 2, 5
KEEN, 1971: 235 - 236; text fig. 584
HERTLEIN & GRANT, 1972: 302 - 303

?*Donax naviculus* Hanley [as *D. "navicula"*] [probably a synonym]

HANLEY, 1845: 15
REEVE, 1854: plt. 4, fig. 18
CARPENTER, 1857b: 186, 229, 246, 279, 304
CARPENTER, 1857c: 50
CARPENTER, 1864: 537, 541, 620, 640 [1872: 23, 27, 106, 126]
SOWERBY, 1866: 314; plt. 3, fig. 80
BERTIN, 1881: 66, 97
HERTLEIN & STRONG, 1949: 254, 258; plt. 1, fig. 1
OLSSON, 1961: 341, 533; plt. 60, figs. 3, 3a
KEEN, 1971: 237 - 238; text fig. 593

Type Material:

Donax californicus – Lost, but CONRAD's (1837) description and 23 mm-long figure are sufficient to identify the taxon. Twelve specimens in BM (NH) Nuttall collection 61.5.20.91 (Figure *3*), thought by Nuttall, Carpenter, and KEEN (1966: 170) to have been the type material, are really *Donax gouldii* Dall, 1921. Conrad's figure: Figure *4*.

Donax naviculus – BM(NH), without registry number, **lectotype** herein, the larger of 2 specimens, pair, 24.5 mm; **paralectotype**, a smaller right valve. Figure *5*.

Type Localities:

Donax californicus – Near Santa Barbara, California, in sand; T. Nuttall.

Donax naviculus – Golfo de Nicoya, Costa Rica; H. Cuming.

Nomenclatural Commentary:

As discussed previously, due to a misinterpretation of type material, *Donax gouldii* went under the name *D. californicus* for a time. However, this is not the only nomenclatural complication.

Perhaps in an attempt to interpret Conrad's type figure, SOWERBY (1866) used the name *Donax californicus* for what we now call *Donax contusus* Reeve, 1854, a distinct Panamic species with pits in the interspaces between the radial ribs.

I see little reason to separate the Californian *Donax californicus* from the Panamic *D. naviculus*. The ranges of the species are coterminous, and apparent differences may

Explanation of Figures *1* to *6*

Figure *1*: *Donax gouldii*. Holotype of *Donax gouldii* and **lectotype** (herein) of *Donax obesus* Gould, USNM 664935; 23.2 mm

Figure *2*: *Donax gouldii*. **Lectotype** (herein) of *Donax laevigatus* Reeve, specimen on left, BM(NH) without registry number; 23 mm. The two specimens on right are **paralectotypes**

Figure *3*: *Donax gouldii*. Specimen in Nuttall collection, BM(NH) 61.5.20.91, labeled "*Donax californica* Conr."; card measures 72 mm across

Figure *4*: *Donax californicus*. Conrad's original illustration; 23 mm

Figure *5*: *Donax naviculus* (? = *D. californicus*). **Lectotype** (herein) of *Donax naviculus*, BM(NH), without registry number; 24.5 mm

Figure *6*: *Donax californicus*. Hypotype, CASGTC 53333, San Pedro, California; 23.5 mm

Figure *1*

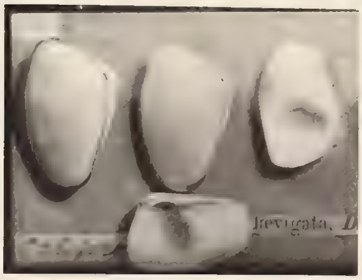

Figure *2*

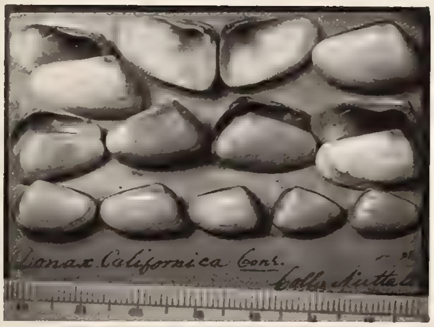

Figure *3*

Figure *4*

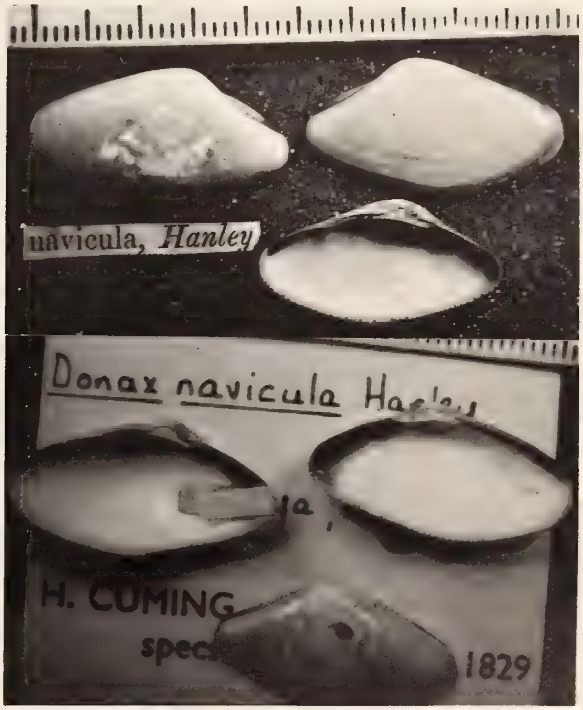

Figure *5*

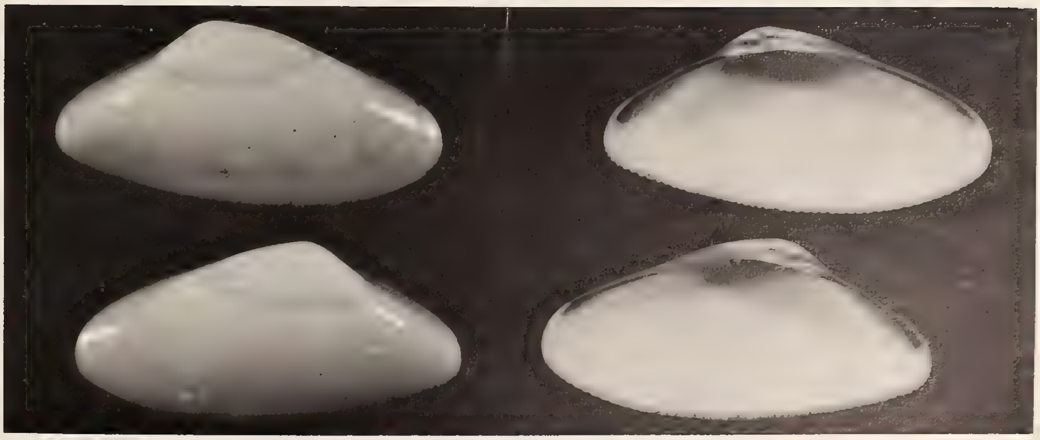

Figure *6*

be clinal. Panamic material averages larger, is more triangular, and is more concave postero-dorsally. HANLEY (1845), in fact, compared *D. naviculus* to *D. californicus*, indicating that the former was "more triangular." A statistical study is needed to elucidate properly the relationship between the two taxa. In the meanwhile, Californian records of *D. naviculus* (CARPENTER, 1864: 640; and COOPER, 1867) may be dismissed and the name restricted to material from south of Bahía Magdalena, Baja California Sur.

Donax flexuosus Gould, 1853, was described from "Santa Barbara," California, but this was in error. The type specimens are, in reality, *D. striatus* Linnaeus, 1767, from the Caribbean, and a lectotype has been designated and illustrated by JOHNSON (1964). Perhaps because of the use of the name *D. californicus* for the wrong Californian species and a "process of elimination," the name *Donax flexuosus* was used by some workers (COOPER, 1867, 1888; WILLIAMSON, 1892) for the true *D. californicus*.

CARPENTER (1857b) reported the similar species *Donax gracilis* Hanley, 1845, from California based on Jewett's collection. Later (1864), he suggested that the specimens were probably from the Panamic province. *Donax gracilis* is not known from north of Bahía Magdalena, Baja California Sur (KEEN, 1971), and is characteristic of more open coast than *D. naviculus* (HOFFSTETTER, 1952). It is longer, narrower, more evenly curved ventrally, less inflated, and more shiny than *D. naviculus* (OLSSON, 1961; KEEN, 1971).

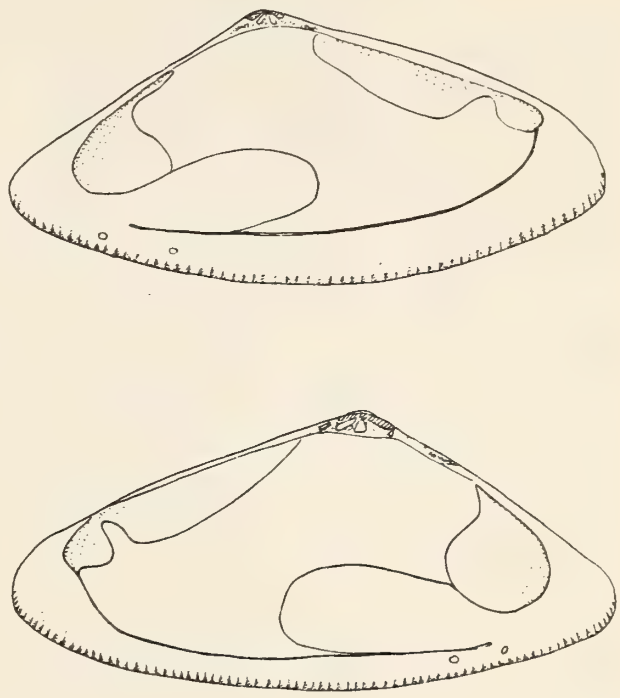

Figure 8

Donax californicus
internal view of valves, SU 51, San Pedro, California

Description:
Medium-sized for genus (to 25 mm, but up to 33 mm); elongate; moderately inflated; relatively thin; anterior end longer, produced, rounded; bluntly pointed posteriorly; ventral edge evenly rounded to flexed a little anterior to beaks; surface relatively smooth, shiny, but with faint radial sculpture; periostracum thin, adherent, tan, shiny; dorsal margins rayed with dark stripes; interior ventral margin roughened by ends of radial sculpture. Other internal details as in Figure 8; see also Figure *6*.

Geographic Distribution and Ecology:
Santa Barbara, California (CONRAD, 1837, but not collected in recent years); Point Mugu, California (USNM 348175), to Bahía Magdalena, Baja California Sur (MCZ 71141; ANSP 225916; and many other lots), with many intermediate records; presumably to Tumbez, northern Peru (OLSSON, 1961), if *Donax naviculus* is ranked as a synonym or subspecies. This species occurs from the intertidal zone to 5 m, in sandy mud, in protected environments such as near bay or estero entrances (WEYMOUTH, 1921; BURCH, 1945a; FITCH, 1953).

Material seen:
92 lots from north of Bahía Magdalena.

Geologic Distribution and Biogeography:
In the late Pleistocene, *Donax californicus* is known from the Baldwin Hills, California (WILLETT, 1937; BURCH, 1947), to Bahía Magdalena, Baja California Sur (JORDAN, 1936). (*Donax naviculus* has been recorded from the late Pleistocene of Santa Elena, Ecuador, by HOFFSTETTER [1952]). It has also been reported in the early Pleistocene of the San Pedro area, California (ARNOLD, 1903; T. OLDROYD, 1925; BURCH, 1947), and from a transitional Plio-Pleistocene formation of southern California (PRESSLER, 1929). Records of this species from the Pliocene of San Diego, California (COOPER, 1888 [as *D. flexuosus*]; Dall, 1900) have not been confirmed in recent years (HERTLEIN & GRANT, 1972).

Thus, it appears that *Donax californicus* may be an early Pleistocene arrival to our fauna and presumably of Panamic origin.

OTHER SPECIES

Three other specific names have been recorded as Californian:

(1) *Donax punctatostriatus* Hanley, 1843, has been reported from San Pedro, California (DALL, 1916, 1921), but I have seen no specimens in any collection to confirm this record. CARPENTER's (1864) record from Isla Cedros, Baja California Norte, is confirmed by a specimen in the Philadelphia Academy of Natural Sciences (ANSP 52-963), and a specimen in the Berry collection extends the known distribution to Isla Guadalupe, Baja California Norte.

In spite of its presence in the northern portion of the Panamic province, *Donax punctatostriatus* has not been recorded from the warm water late Pleistocene of southern California. For these reasons, I agree with STRONG (1924), GRANT & GALE (1931), and BURCH (1945a) in concluding that this species should not be considered a member of the Californian fauna.

(2) *Donax conradi* Reeve, 1854, *ex* Deshayes MS, now ranked as a junior subjective synonym of *D. contusus* Reeve, 1854, by KEEN (1971), was reported from "California" by DESHAYES (1855) and from San Pedro, California, by DALL (1916, 1921). Deshayes' record was simply lack of precision. Dall's record probably was in error since there are no specimens from California in any of the collections I have examined. *Donax contusus* occurs only as far north as the southern part of the Gulf of California (KEEN, 1971). The conclusion to exclude this species from the Californian province was also reached by STRONG (1924), GRANT & GALE (1931), and BURCH (1945a).

(3) *Donax rostratus* C. B. Adams, 1852a, was reported from Santa Barbara, California, by CARPENTER (1857b) based on the Jewett collection. Later he noted that these specimens were actually from Acapulco, Mexico (CARPENTER, 1864).

ECOLOGY AND BIOGEOGRAPHY

So that they may be compared with information published for the 3 other tellinacean families, the ecological data about the two species of northwest American Donacidae are summarized as follows:

Table 1

Species	Depth range meters	Bottom type	Coastal exposure
Donax gouldii	0 - 5	fine sand	exposed to semi-protected
Donax californicus	0 - 5	sandy-mud	protected

The relative abundance of the two species is reflected in their frequency in museum collections:

Table 2

Species	Number of lots seen
Donax gouldii	221
Donax californicus	92 [1]

[1] not including specimens from Panamic province south of area of study (assuming *D. naviculus* is a synonym)

Defining the boundary between the Oregonian and Californian provinces as Point Conception, California, and that between the Californian and Panamic provinces as Punta Eugenio, Baja California Sur, the faunal relationships of the two species may be indicated as follows:

Table 3

Oregonian	Californian	Panamic
3. *Donax gouldii*		
	2. *Donax californicus*	=?*D. naviculus*

In this table, the following abbreviations are used:
2. species occurring in 2 provinces
3. species occurring in 3 provinces

Reported distributions in the late Pleistocene are similar to distributions in the Recent fauna. *Donax gouldii* appears in the Pliocene, while *D. californicus* is first known from near the Plio-Pleistocene boundary. The relation of both to earlier species remains unclear. The affinity of *D. californicus* to Panamic species is certain, while the biogeographic relations of *D. gouldii* are unknown.

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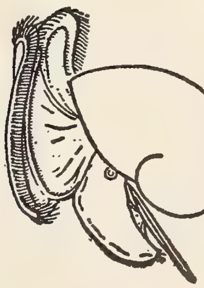

Techniques for Photographing Modern Mollusks [1]

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(1 Plate)

INTRODUCTION

MANY PHOTOGRAPHERS HAVE experienced difficulty in photographing modern mollusks for illustrating malacological reports. Critical morphological features such as dentition and sculpture are frequently lost in conventional photography because of lustrous surfaces, whiteness, or translucency of the specimens. One of the most common problems is the loss of surficial details in the glare caused by reflection from the light sources. These problems have often made it necessary to retouch photographs of modern pelecypods and gastropods to provide satisfactory illustrations for scientific publications.

This report describes and illustrates some techniques for producing high-quality photographs of modern mollusks that do not require retouching. These techniques, equally applicable to photography of fossils, involve coating the surface of a shell with various substances prior to photography. Customarily, modern mollusks are photographed without applying any coating to the shell surfaces, whereas fossil invertebrates are frequently coated with substances such as ammonium chloride (KIER, GRANT, & YOCHELSON, 1965) before photographing, to improve the quality of the photograph.

These techniques are illustrated by selected photographs of a few modern mollusks (Figures *1* - *18*) that are arranged to contrast various coating techniques with conventional (uncoated) photographs. Specimens of *Cassis* and *Oliva* in the top 2 rows (Figures *1* - *8*) have been photographed using 3 different techniques but under identical lighting conditions. Figures *1* and *5* are photographed without any coating; Figures *2* and *6* are coated with a dulling spray; Figures *3* and *7* are coated with ammonium chloride (whitening technique); and Figures *4* and *8* are coated with black opaque, dried, and then dusted with ammonium chloride. The rest of the specimens (Figures *9* to *18*) are photographed either naturally (untreated) (Figures *9, 10, 13, 14,* and *17*) or after they were coated with black opaque and then dusted with ammonium chloride (Figures *11, 12, 15, 16,* and *18*). These are arranged in pairs to show the advantages of the black opaque technique described below. Explanations of the 3 different techniques of coating shells are also given.

DULLING SPRAY TECHNIQUE

Use of dulling spray on the specimens (Figures *2* and *6*) eliminates much of the glare from reflecting surfaces, but the representation of textural details (relief), especially on white shells or on whitish areas of many specimens, is not significantly improved compared with the untreated specimens (Figures *1* and *5*). For example, the denticles on the outer lip of the *Cassis* are washed out in both Figures *1* and *2*. An advantage of this technique, however, is that it does not conceal color patterning, and in photographing uniformly darker colored shells such as the *Oliva* (Figure *6*), it serves quite adequately. After photography this substance can be removed with a solvent such as acetone. The brand name of the spray is Krylon Dulling Spray No. 1310, manufactured by Krylon, Inc., Norristown, Pennsylvania.

AMMONIUM CHLORIDE (WHITENING) TECHNIQUE

Application of ammonium chloride sublimate (KIER, GRANT, & YOCHELSON, 1965), a technique commonly

[1] Publication authorized by the Director, U. S. Geological Survey

used in photography of fossil specimens, eliminates glare to an even greater extent than does the dulling spray. Color patterns, however, are diminished in clarity (compare Figures *1* and *5* with Figures *3* and *7*). This technique is also superior to the use of dulling spray in bringing out textural details (compare Figures *2* and *3*) and the coating can be easily removed by rinsing the specimen in water.

BLACK OPAQUE TECHNIQUE

This technique involves coating dry specimens with black opaque, applied with a small brush. It can be diluted with water to the desired consistency each time it is used, and it dries quickly. The brand of black opaque used in coating these specimens is Rogersoll G-88, manufactured by Harry H. Roger, Inc., 5331 S. Cicero Avenue, Chicago, Illinois.

After the opaque has dried thoroughly, the specimen is dusted with a thin film of ammonium chloride sublimate delivered from a spray gun (Sakamoto, 1970); it is then ready for photography.

When photography has been completed, the opaque can be easily cleaned off the specimen with water and a soft brush. Some specimens, however, are more difficult to clean than others; such specimens can be immersed in warm water to which a small amount of sodium hydroxide has been added, and then agitated in an ultrasonic cleaner for a few minutes.

Photographs made using this technique are exceptionally sharp and clear. For example, the denticles on the aperture of the cassidid gastropod are clearly discernible (Figure *4*), whereas many of them are extremely difficult to detect on the uncoated view (Figure *1*). The contrast between this technique and photographs of untreated specimens is further illustrated by Figures *5* and *8, 9* and *12, 10* and *11, 13* and *16, 14* and *15,* and *17* and *18*. The potential of the black opaque technique in the photography of bivalve interiors, as illustrated by the *Dosinia* (Figures *13* and *16*) and the *Macoma* (Figures *17* and *18*), is clearly shown by the sharp and detailed photographs of the pallial sinus, muscle scars, and dentition; these features can be accurately shown without retouching the photograph or outlining these features prior to photography. Photographs made with the black opaque technique are clearly superior to those in which the specimens are photographed without any preparation or either of the other techniques.

Coating translucent or thin specimens with black opaque also prevents light from passing through the specimen when the white background technique (Sakamoto, 1970) is used to obtain an initial white margin around the specimen. Black opaque is superior to semi-permanent ink or dyes as an undercoating because the opaque can be easily washed off a specimen.

However, the black opaque technique completely masks color patterning. For specimens with color patterning 2 photographs of each specimen can be combined – one treated with the dulling spray to show the color patterning and the other coated with the combination of black opaque and ammonium chloride to show sculptural and textural details.

WHITE BACKGROUND TECHNIQUE

Modern mollusks are generally illustrated on a white background in published reports. The specimens, however, are usually photographed against a dark background. This undesirable background can best be eliminated by a simple photographic procedure – the white background technique (Sakomoto, 1970: D231 - D232). In this technique the specimen is placed on a small light-box (15 cm square) and held in place with a lump of modeling clay and photographed. Next the room is darkened and the dark area surrounding the object on the negative is re-exposed by illuminating the light-box (the object remaining in place) for about 20 seconds. The light source is an internally mounted, transformer-controlled 40-watt bulb; the light-box is topped with a pane of frosted glass. This technique saves considerable time in preparing illustrative plates and provides a more accurate outline of specimens than trimming with scissors or applying opaque to the negative.

CONCLUSION

Photography of modern mollusk shells using a combination of the black opaque technique and subsequent whitening with ammonium chloride produces high-quality photographs that do not require retouching. The photographs are of uniform tone and show excellent definition, sharpness, resolution, and contrast. These techniques eliminate glare and mottling. If color patterning should be shown, a second photograph of the specimen coated with dulling spray can be prepared. The black opaque technique is especially advantageous for obtaining an original white background and for photographing fossils with pronounced color mottling.

ACKNOWLEDGMENTS

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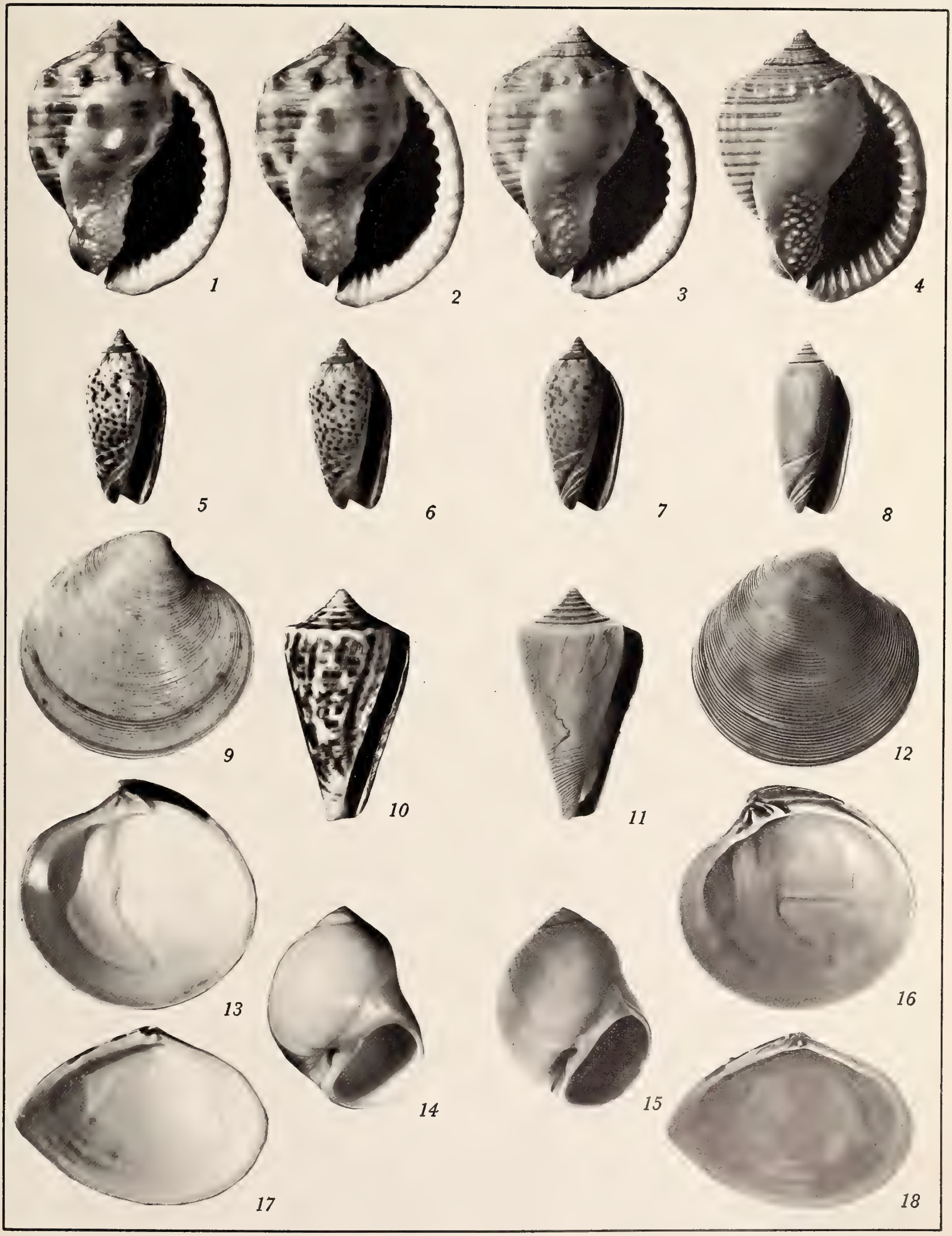
Explanation of Figures *1* to *18*

(all figures natural size)

Figures *1* to *4*: *Cassis* sp., Baja California, Mexico. *1* untreated; *2* coated with dulling spray; *3* coated with ammonium chloride; *4* coated with black opaque and ammonium chloride.
Figures *5* to *8*: *Oliva* sp., Baja California, Mexico. *5* untreated; *6* coated with dulling spray; *7* coated with ammonium chloride; *8* coated with black opaque and ammonium chloride.
Figures *9, 12, 13,* and *16*: *Dosinia* sp., Baja California, Mexico. *9, 13,* untreated; *12, 16,* coated with black opaque and ammonium chloride.
Figures *10* and *11*: *Conus* sp., Baja California, Mexico. *10* untreated; *11* coated with black opaque and ammonium chloride.
Figures *14* and *15*: *Polinices* sp., Baja California, Mexico. *14* untreated; *15* coated with black opaque and ammonium chloride.
Figures *17* and *18*: *Macoma* sp., Gulf of Alaska, Alaska. *17* untreated; *18* coated with black opaque and ammonium chloride.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A Census of Marine Prosobranch Gastropods at San Diego, California

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(1 Map)

INTRODUCTION

San Diego, situated in the extreme southwestern corner of the United States, has long been an important port. Much of the early collecting of west coast molluscs was centred there. When the taxonomic phase of molluscan studies reached its height in the last century many new species were named from specimens collected in the area. For this reason, references to San Diego are frequent in the taxonomic literature and material from the area has reached museums in many parts of the world.

Around the turn of the century, a number of workers compiled lists of molluscs specifically from San Diego. The important lists are those of Orcutt & Dall (1885), Kelsey (1907), Smith (1907), and Baily (1907). Additional notes were also presented by Kelsey (1898) and Orcutt (1919, 1922). Farmer (1964) included molluscs in his illustrated paper on common marine animals of San Diego. Human (1970) has given a list of shells obtained from gravel at Bird Rock, La Jolla.

We present a list of prosobrasch gastropods recorded from the San Diego area during the last few years. Since the total molluscan fauna was considered too large for detailed study, the prosobranch gastropods were selected as a conveniently sized group, and one which is of particular significance in ecological studies. Deepwater species are not included, and the emphasis is on the species of the intertidal and shallow sublittoral zones. The list has been compiled from our observations in the period August 1970 to August 1971, and from specimens and notes kindly made available to us by members of the San Diego Shell Club. The list does not claim to be exhaustive since some of the smaller and rarer species are bound to be overlooked.

DESCRIPTION of the CENSUS AREA

Rather than giving a complete list of localities where each species has been recorded we decided to divide the chosen area into six parts (Figure 1). The northern boundary was the San Diego City limits south of Del Mar and the southern boundary was the 28th Street Pier, San Diego. The southern part of San Diego Bay, Coronado and Imperial Beach were not examined in the present survey.

Area 1: This extends from the San Diego City Limits south of Del Mar to the beginning of the rocky area at La Jolla Beach and Tennis Club. This Area consists of an exposed sandy beach backed by cliffs along much of its length. Solid substrata are provided by a few outcroppings of hard conglomerate, some large boulders, and the pier pilings of the Scripps Institution of Oceanography. Few gastropods inhabit the sand itself. The pelagic snail *Janthina* has washed ashore here.

Area 2: This extends from the beginning of the rocky area at La Jolla Beach and Tennis Club to the end of the intertidal rocky area at Tourmaline Canyon, Pacific Beach. It is the richest and most diverse of the areas. There are rocky coves with sandy beaches separated by rocky points and low cliffs. On rocks at the splash and high tide levels may be found *Littorina* and various limpets of the genus *Collisella.* On rocks and in pools at the mid-tide level are several species of *Tegula* feeding on microscopic algae, and *Acanthina* feeding on barnacles. On exposed rocks *Lottia* may be prominent, and in crevices *Haliotis cracherodii* may be found. *Fissurella volcano* lives under rocks in more sheltered localities. *Serpulorbis squamigerus* forms massive colonies in some places. Small gastropods

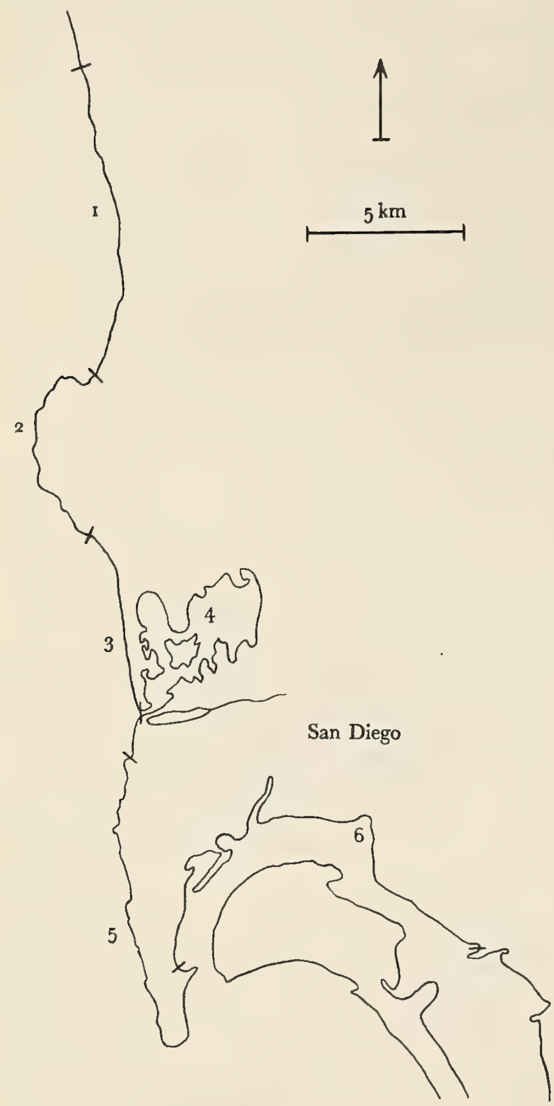

Figure 1

The census areas at San Diego, with their reference numbers.

find food and shelter amongst the *Mytilus californianus* beds. At the low tide level the fauna is richer and the habitats are more diverse. In sand around rocks are to be found *Maxwellia gemma, Macron, Olivella, Conus* and *Pseudomelatoma. Megathura* and *Astraea undosa* can be found grazing on algae on rocks, and *Haliotis fulgens* is common in the vicinity of rock crevices and overhangs. Under stones resting on sand or gravel, especially in rock pools, are to be found a large variety of smaller forms including *Homalopoma, Seila, Amphissa, Nassarina, Volvarina* and *Mitromorpha.* The sand itself contains *Vitrinella, Teinostoma, Caecum* and *Fartulum. Epitonium* and *Opalia* are found at the base of sea anemones. The surf grass *Phyllospadix* forms beds at the low tide level, and the limpet *Notoacmea paleacea* lives on the leaves. The roots and associated sand form a sheltered habitat for many of the small species mentioned above. The brown alga *Egregia* supports *Notoacmea insessa* on the stipes, and *Norrisia* and the associated *Crepidula norrisiarum* on the thalli. Species of *Tricolia, Lacuna, Barleeia,* and *Mitrella* are common on plants. In the shallow subtidal zone at 6 to 9 m depth are found *Haliotis corrugata, Kelletia, Erato, Trivia,* and *Cypraea.* At greater depths of about 21 m live *Haliotis assimilis, H. sorenseni* and *Pteropurpura macroptera,* and in addition some species which occur intertidally in Northern California such as *Haliotis rufescens, Diodora aspera, Acmaea mitra* and *Astraea gibberosa.* Gravel from this depth contains a number of characteristic small species such as *Homalopoma paucicostatum* and *Caecum dalli.*

Area 3: This extends from the end of the rocky intertidal area at Tourmaline Canyon to the beginning of the rocky intertidal area at Ocean Beach Municipal Pier. It consists of an exposed sandy beach supporting a sparse molluscan fauna. Shells of species inhabiting offshore sandy bottoms, including *Bursa, Nassarius, Cancellaria,* and *Ophiodermella* are washed up here. On the jetties a limited fauna is to be found, including notably *Thais emarginata* which is rather uncommon in Southern California.

Area 4: This includes the whole of Mission Bay, its Entrance Channel and the Flood Control Channel of the San Diego River. In brackish water, where the San Diego River mixes with sea water, *Tryonia* is found. In the salt marshes *Assiminea* occurs on damp mud under plants or debris, and on the mud flats at high tide level *Cerithidea* is abundant. In some sandy subtidal areas *Bittium, Polinices, Nassarius, Olivella,* and *Conus* are common. There are beds of the eelgrass *Zostera,* with the limpet *Notoacmea depicta* on the leaves, accompanied by a number of small snail species such as *Tricolia compta, Lacuna, Barleeia subtenuis, Mitrella* and *Granulina.* A characteristic fauna is found on the artificial rocky jetty and pilings of the Bay. There are, in addition to the *Collisella, Tegula* and *Littorina* of the outer coast, well grown specimens of the predatory species *Ceratostoma, Pteropurpura festiva, Ocenebra poulsoni,* and *Acanthina.* Rocks and shell debris provide substrates for *Crepidula onyx, Crepipatella,* and *Crucibulum.*

Area 5: This extends from the beginning of the rocky intertidal zone at Ocean Beach Municipal Pier to Ballast Point at the entrance to San Diego Bay. Much of the area consists of steep cliffs dropping more or less directly into the sea, and the intertidal area is small and exposed to heavy surf. There is a gently sloping, more sheltered intertidal area near the Point Loma Lighthouse. The fauna is similar to that of Area 2, but lacks the species requiring more sheltered habitats.

Area 6: This extends along the north shore of San Diego Bay from Ballast Point to 28th Street Pier, San Diego. It is a sheltered bay environment and consists of stretches of sand and mud with pilings and jetties. There is some pollution. The fauna is a reduced version of that found in Mission Bay in Area 4.

SYSTEMATIC ACCOUNT

The following information is included in the systematic account:

1. The scientific name. The nomenclature follows the work of McLean (1969). In the case of the few species not listed by McLean, a reference is given to the original description, or to a convenient secondary source. All entries in the census are based on specimens seen by us, ensuring a consistency in identification and nomenclature.

2. The observed habitat and substrate, and an indication of tidal level within the categories brackish water, splash zone, high tide, mid-tide, low tide, and subtidal.

3. The census area, followed by a named locality. The name is omitted in the case of species which are very widespread, or in the case of rare species which might be endangered by revealing a locality. When a name is included it is not intended to imply that this is the only place in the Area where a species can be found. Rather it is given as an example.

4. A subjective estimate of relative abundance on the scale abundant, common, occasional, rare.

5. The most recent year of observation.

6. The collector. Any entry not attributed to a collector represents our own observations. The following members of the San Diego Shell Club contributed records, and are denoted in the list by initials.

BD	Dilworth, Billee
FBG	Good, Frank H. and Barbara
JCH	Hertz, Jules and Carole M.
CCM	Martin, Clifford and Clifton
JNM	Michel, John and Nola
DMM	Mulliner, David and Margaret
JBM	Myers, John and Barbara

Haliotidae

Haliotis assimilis Dall, 1878
On rock surfaces, subtidal at 18 m depth. 2, off Bird Rock, occasional, 1971, DMM; 5, off Point Loma, occasional, 1970, JNM.
Haliotis corrugata Wood, 1828
On rock surfaces, subtidal at 9 to 15 m depth. 2, off Bird Rock, common, 1971, DMM; 5, off Point Loma, common, 1970, JNM.
Haliotis cracherodii Leach, 1814
In rock crevices and under ledges, mid- to low tide. 2, La Jolla Cove, common, 1970; 4, Quivira Basin, occasional, 1965, JCH.
Haliotis fulgens Phillipi, 1845
In rock crevices and under ledges, low tide to subtidal. 2, common, 1971; 4, Entrance Channel, occasional, 1971; 5, common, 1971.
Haliotis rufescens Swainson, 1822 [see Cox, 1960]
On rock surfaces, subtidal at 15 m depth. 2, off Bird Rock, common, 1971, DMM; 5, off Point Loma, common, 1970, JNM.
Haliotis sorenseni Bartsch, 1940. On rock surfaces, subtidal at 18 m depth. 5, off Point Loma, occasional, 1970, JNM.

Scissurellidae

Sinezona rimuloides (Carpenter, 1865)
In sand around *Phyllospadix* roots, low tide. 2, Bird Rock, rare, 1967, FBG.

Fissurellidae

Diodora arnoldi McLean, 1966
3, Tourmaline Surfing Beach, dead shells only, 1971.
Diodora aspera (Rathke, 1833)
On rocks, low tide. 4, Quivira Basin, rare, 1970, JCH.

Megathura crenulata (Sowerby, 1825)
On rock surfaces, low tide. 2, Beach and Tennis Club, occasional. 1971; 4, Vacation Isle, occasional, 1971; 5, Sunset Cliffs, abundant, 1971; Point Loma, occasional, 1971.
Megatebennus bimaculatus (Dall, 1871)
Under boulders, low tide to subtidal. 2, Bird Rock, rare, 1971; 4, Quivira Basin, rare, 1969, FBG; Entrance Channel, rare, 1969, JCH.
Lucapinella callomarginata (Dall, 1871)
Under boulders, low tide. 4, Quivira Basin, rare, 1964, FBG; Vacation Isle, rare, 1971, JCH.
Fissurella volcano Reeve, 1849
On rocks and under boulders, mid- to low tide. 2, common, 1971; 5, Point Loma, common, 1971.

Acmaeidae

Acmaea mitra Rathke, 1833
On rocks under kelp, subtidal at 18 m depth. 5, off Point Loma, occasional, 1971, JNM.
Acmaea rosacea Carpenter, 1864
2, off Bird Rock, dead shells from subtidal gravel; off Point Loma, 18 m depth, 1966, FBG.
Collisella asmi (Middendorf, 1847)
Attached to shells of *Tegula funebralis* or *T. eiseni* either living or containing hermit crabs, mid-tide. 2, Beach and Tennis Club, occasional, 1971; Bird Rock, common, 1971.
Collisella conus (Test, 1945)
On rock surfaces, high to mid-tide. 2, Bird Rock, common, 1971; 4, Entrance Channel, common, 1971; 5, Point Loma, common, 1971.
Collisella digitalis (Rathke, 1833)
On rock surfaces, splash zone to high tide. 2, abundant, 1971; 5, abundant, 1971.
Collisella limatula (Carpenter, 1864)
On rock surfaces, mid-tide. 2, abundant, 1971; 5, abundant, 1971.
Collisella pelta (Rathke, 1833)
On stipes of *Egregia,* mid- to low tide. 2, La Jolla Cove, occasional, 1971.
Collisella scabra (Gould, 1846)
On rock surfaces, high to mid-tide. 2, abundant, 1971; 4, abundant, 1971; 5, abundant, 1971.
Collisella strigatella (Carpenter, 1864)
In boulders set in sand, mid-tide. 2, Beach and Tennis Club, common, 1971; 3, Tourmaline Surfing Beach, common, 1971.
Notoacmea depicta (Hinds, 1842)
On blades of *Zostera,* low tide. 4, common, 1971.
Notoacmea insessa (Hinds, 1843)
On stipes and holdfasts of *Egregia,* low tide. 2, common, 1971; 4, Entrance Channel, common, 1971; 5, Sunset Cliffs, common, 1971.
Notoacmea paleacea (Gould, 1853)
On blades of surf grass *Phyllospadix,* low tide. 2, common, 1971.
Lottia gigantea Sowerby, 1834
On rock surfaces, high to mid-tide. 2, La Jolla Cove, common, 1971; 5, common, 1971.

Trochidae

Calliostoma annulatum (Lightfoot, 1786)
2, La Jolla Cove, dead shells only, 1970.
Calliostoma gemmulatum Carpenter, 1864
3, Tourmaline Surfing Beach, dead shells only, 1971.
Calliostoma gloriosum Dall, 1871
Under rocks, low tide to subtidal. 2, off Bird Rock, 21 m depth, rare, 1971, DMM; 4, Quivira Basin, low tide, rare, 1966, FBG.
Calliostoma supragranosum Carpenter, 1864
Under rocks, low tide to subtidal. 4, low tide, occasional, 1968, FBG; 5, off Ocean Beach, 19.5 m depth, 1965, BD.
Calliostoma tricolor Gabb, 1865
4, Quivira Basin, one individual on a rock under algae, low tide, 1970, JCH.
Turcica caffea Gabb, 1865
5, off Ocean Beach, one individual at 22.5 m depth, 1969, FBG.
Norrisia norrisi (Sowerby, 1838)
On brown algae, low tide to subtidal. 2, La Jolla Cove, common, 1971; 4, Flood Control Channel, common, 1971; 5, Sunset Cliffs, common, 1971.
Tegula aureotincta (Forbes, 1852)
Under and around rocks, mid- to low tide. 2, La Jolla Cove, occasional, 1971; Bird Rock, common, 1971; 5, Point Loma, occasional, 1971.
Tegula eiseni Jordan, 1936
Under and around rocks, mid- to low tide. 2, abundant, 1971; 4, Entrance Channel and Flood Control Channel, abundant, 1971; 5, Point Loma, abundant, 1971.
Tegula funebralis (A. Adams, 1855)
On rocks, mid-tide. 1, rocks north of Scripps Pier, abundant, 1971; 2, 4, 5, abundant, 1971; 6, Shelter Island, abundant, 1967, JCH.
Tegula gallina (Forbes, 1852)
On rocks, mid-tide. 1, Torrey Pines Beach, common, 1962, FBG; 2, Bird Rock, dead shells only, 1970.
Tegula regina (Stearns, 1892)
On rocks, low tide (exceptionally) to subtidal. 4, Entrance Channel, rare, 1971.
Halistylus pupoideus (Carpenter, 1864) [see Grant & Gale, 1931]
In gravel, low tide. 2, La Jolla Cove, occasional, 1971.

Skeneidae

Parviturbo acuticostatus (Carpenter, 1864)
In gravel around *Phyllospadix* roots, low tide. 2, rare, 1970, FBG.

Liotiidae

Liotia fenestrata Carpenter, 1864
2, La Jolla Cove, dead shells only, 1970.
Macrarene sp., juv.
4, Entrance Channel, dead shell, 1971.

Turbinidae

Homalopoma fenestratum (Dall, 1919)
2, La Jolla Cove, dead shells only, 1971.
Homalopoma luridum (Dall, 1885)
Under rocks, low tide. 2, La Jolla Cove, common, 1971; Bird Rock, common, 1971; 5, Point Loma, common, 1971.
Homalopoma paucicostatum (Dall, 1871)
2, off Bird Rock, dead shells in gravel from 18 m depth, 1971.
Astraea gibberosa (Dillwyn, 1817)
On and around rocks, subtidal at 21 m depth. 2, off Bird Rock, common, 1971, DMM; 5, off Point Loma, occasional, 1970, JNM.
Astraea undosa (Wood, 1828)
On and around rocks in sand, low tide. 2, common, 1971; 4, Flood Control Channel, abundant, 1971; 5, common, 1971.

Phasianellidae

Tricolia compta (Gould, 1855)
On blades of *Zostera*, low tide. 4, Flood Control Channel, rare, 1971.
Tricolia pulloides (Carpenter, 1865)
On plants, low tide. 2, Beach and Tennis Club, occasional, 1971; Bird Rock, common, 1966, FBG; 5, Point Loma, common, 1967, FBG
Tricolia rubrilineata (Strong, 1928)
On plants, low tide. 2, abundant, 1971; 5, Sunset Cliffs, common, 1971.

Lacunidae

Lacuna unifasciata Carpenter, 1857
On plants, low tide. 2, abundant, 1971; 4, Flood Control Channel, common on *Zostera*, 1971; 5, Sunset Cliffs, common, 1971.

Littorinidae

Littorina planaxis Phillipi, 1847
On rocks, splash zone to high tide. 2, abundant, 1971; 5, abundant, 1971.
Littorina scutulata Gould, 1849
On rocks, high to mid-tide. 2, abundant, 1971; 4, abundant, 1971; 5, abundant, 1971.

Hydrobiidae

Tryonia imitator Pilsbry, 1877
In sand or mud, brackish water. 4, Flood Control Channel between 50 and 250 m west of Highway 5, common, 1971.

Truncatellidae

Truncatella californica Pfeiffer, 1857
Under plants or rubble, above high tide. 4, Crown Point, abundant, 1963, CCM (dead shells only, 1971).

Rissoidae

Alvinia aequisculpta (Keep, 1887)
On plants or in gravel, low tide. 2, Bird Rock, occasional, 1971.
Barleeia californica Bartsch, 1920
On algae, low tide. 2, abundant, 1971.
Barleeia haliotiphila Carpenter, 1864
On algae, low tide. 2, abundant, 1971.
Barleeia subtenuis Carpenter, 1864
On plants, low tide. 4, abundant, 1971.

Assimineidae

Assiminea californica Tryon, 1865
Under stones or debris at high tide, or on mud under plants in salt marsh. 2, foot of Archer Street, common under boulders with *Pedipes*, 1971; 4, Flood Control Channel, common, 1971.

Vitrinellidae

Vitrinella oldroydi Bartsch, 1907
In sand, especially that trapped around plants or under boulders, low tide. 2, Bird Rock, occasional, 1971.
Teinostoma supravallatum (Carpenter, 1864)
In sand, especially that trapped around plants or under boulders, low tide. 2, Bird Rock, occasional, 1971.

Caecidae

Caecum californicum Dall, 1885
In sand, low tide to subtidal. 2, common, 1971.
Caecum crebricinctum (Carpenter, 1864)
In sand or gravel, especially under and around rocks, low tide to subtidal. 2, Beach and Tennis Club, common, 1971.
Caecum dalli Bartsch, 1920
In sand or gravel, sublittoral at 21 m depth. 2, off Bird Rock, occasional, 1971.
Fartulum hemphilli Bartsch, 1920
In sand or gravel, low tide to subtidal. 2, occasional, 1971.
Fartulum occidentale Bartsch, 1920
In sand or gravel, low tide. 2, Beach and Tennis Club, rare, 1971.

Vermetidae

Serpulorbis squamigerus (Carpenter, 1857)
Attached to rocks, mid-tide. 2, 4, 5, common, 1971.

Potamididae

Cerithidea californica (Haldeman, 1840)
On mud or muddy sand, high tide. 4, 6, abundant, 1971.

Cerithiidae

Bittium interfossa (Carpenter, 1864)
In sand, subtidal at 12 m depth. 5, off Ocean Beach, occasional, 1967, FBG.
Bittium quadrifilatum (Carpenter, 1864)
In sand, subtidal at 1.5 m depth. 4, Flood Control Channel, abundant, 1971.

Cerithiopsidae

Cerithiopsis carpenteri Bartsch, 1911
On yellow sponges attached to stones, low tide. 4, Vacation Isle, common, 1971.
Metaxia convexa (Carpenter, 1857)
2, La Jolla Cove, dead shells only, 1971,
Seila montereyensis Bartsch, 1907
Under rocks, low tide. 2, Beach and Tennis Club, common, 1971.
Triphora pedroana Bartsch, 1907
2, La Jolla Cove, dead shells only, 1971.

Epitoniidae

Epitonium indianorum (Carpenter, 1864) [see Grant & Gale, 1931]
1, 3, dead shells only, 1971.
Epitonium tinctum (Carpenter, 1864)
Around anemones and in sand of rock pools, low tide. 2, La Jolla Cove, occasional, 1971; 5, Point Loma, occasional, 1971.
Opalia funiculata Carpenter, 1857
In sand in rock pools, low tide. 2, La Jolla Cove, occasional, 1971.
Opalia montereyensis (Dall, 1907)
In sand, subtidal. 2, off Bird Rock in sand from 21 m depth, rare, 1971.

Janthinidae

Janthina prolongata Blainville, 1822 [see Keen, 1971]
A pelagic species washed ashore with Velella. 1, La Jolla Shores, common, 1967, JBM.

Hipponicidae

Hipponix antiquatus (Linnaeus, 1767)
On rock surfaces and under stones, mid-tide. 2, Beach and Tennis Club, occasional, 1971.
Hipponix tumens Carpenter, 1864
Under stones in rock pools, mid-tide. 2, Beach and Tennis Club, rare, 1971.

Calyptraeidae

Crepidula aculeata (Gmelin, 1791)
2, dead shells only, 1971.
Crepidula coei Berry, 1950
2, dead shells only, 1971.
Crepidula norrisiarum Williamson, 1905
On shells, especially *Norrisia,* mid-tide to subtidal. 2, La Jolla Cove, occasional, 1971; 5, Point Loma, occasional, 1967, JCH.
Crepidula onyx Sowerby, 1824
On rocks or other shells, mid-tide. 4, common, 1971; 6, Shelter Island, abundant, 1971.
Crepidula perforans (Valenciennes, 1846)
In shells occupied by hermit crabs, mid-tide. 2, Beach and Tennis Club, common, 1971; 4, Ventura Cove, common, 1968, FBG.
Crepipatella lingulata (Gould, 1846)
On rocks, especially the undersurfaces, mid-tide to subtidal. 2, Bird Rock, common, 1971; 5, Ventura Point, common, 1971.
Crucibulum spinosum (Sowerby, 1824)
On rocks and shells, low tide. 4, Vacation Isle, common, 1971; 6, Shelter Island, abundant, 1971.

Naticidae

Polinices altus (Pilsbry, 1929)
In sand, shallow subtidal. 4, Vacation Isle, occasional, 1971.
Polinices lewisii (Gould, 1847)
In sand, shallow subtidal. 4, Vacation Isle, common, 1971; Ventura Cove, occasional, 1971; Flood Control Channel, occasional, 1971.
Polinices reclusianus (Deshayes, 1839)
In sand, low tide to subtidal. 4, Vacation Isle, abundant, 1971; Flood Control Channel, occasional, 1971; 6, Shelter Island, occasional, 1971.
Sinum scopulosum (Conrad, 1849)
3, Tourmaline Surfing Beach, dead shells only, 1971.

Lamellariidae

Lamellaria diegoensis Dall, 1885
In rock crevices, low tide. 4, Quivira Basin, rare, 1969, JCH; Vacation Isle, rare, 1969, FBG.
Lamellaria sharonae Willett, 1939
On rocks, low tide. 2, La Jolla Cove, rare, 1971; Quivira Basin, rare, 1968, FBG.
Lamellaria stearnsii Dall, 1871
Washed ashore on kelp holdfast. 1, Torrey Pines Beach, 1968, JBM.

Eratoidae

Erato columbella Menke, 1847
In gravel or on rocks or plants, low tide. 2, Bird Rock, rare, 1966, FBG; Windansea Beach, amongst *Mytilus* byssus, mid-tide, rare, 1971.
Erato vitellina Hinds, 1844
On rocks or plants, low tide. 2, Windansea Beach, on algae, rare, 1967, FBG; 4, Quivira Basin, on rocks, rare, 1964, FBG.
Trivia californiana (Gray, 1827)
On rocks, low tide to subtidal. 2, La Jolla Cove, rare, 1965, FBG; 4, Entrance Channel, on orange compound ascidian (the animal was also orange coloured), rare, 1971.
Trivia solandri (Sowerby, 1832)
In rock crevices or under ledges, low tide. 2, La Jolla Cove, rare, 1969, FBG; 4, Quivira Basin, rare, 1964, FBG.

Cypraeidae

Cypraea spadicea Swainson, 1823
Under rock ledges, shallow subtidal. 2, occasional, 1971, FBG; 4, occasional, 1971; 5, common, 1971.

Ovulidae

Simnia vidleri (Sowerby, 1881)
On red gorgonians, at 3 to 4.5 m depth. Rare, 1970, JNM.

Bursidae

Bursa californica (Hinds, 1843)
3, Tourmaline Surfing Beach, dead shells only, 1971.

Muricidae

Ceratostoma nuttalli (Conrad, 1837)
On rocks or pilings, mid- to low tide. 2, common, 1971; 4, abundant, 1971; 5, common, 1971.
Pteropurpura festiva (Hinds, 1844)
On rocks or in sand around rocks, low tide. 2, common, 1971; 4, abundant, 1971; 5, common, 1971.
Pteropurpura macroptera (Deshayes, 1839)
On rocks under kelp at 18 m depth. 5, off Point Loma, rare, 1970, JNM.
Pteropurpura trialata (Sowerby, 1841)
On rocks, low tide to subtidal. 2, La Jolla Cove, low tide, rare, 1970, JCH; 4, Entrance Channel, at 6 to 9 m depth, occasional, 1971.
Ocenebra gracillima Stearns, 1871
Under rocks, low tide. 2, Bird Rock, occasional, 1971.
Ocenebra interfossa (Carpenter, 1864) [see Dall, 1921, plt. 11, fig. 8]
On rocks, low tide. 2, Beach and Tennis Club, rare, 1967, JCH.
Ocenebra minor (Dall, 1919)
2, La Jolla Cove, dead shells only, 1971.
Ocenebra poulsoni (Carpenter, 1864)
On rocks or pilings, low tide. 2, common, 1971; 4, abundant, 1971; 5, common, 1971.
Maxwellia gemma (Sowerby, 1879)
In sand among rocks, low tide. 2, Beach and Tennis Club, occasional, 1971; La Jolla Cove, rare, 1971; 4, Quivira Basin, rare, 1970, JCH.
Maxwellia santarosana (Dall, 1905)
On rocks, usually subtidal. 2, Windansea Beach, low tide, rare, 1971, JCH; 4, Entrance Channel, at 3 m depth, rare, 1970.
Acanthina paucilirata (Stearns, 1871)
On rocks, mid-tide. 1, common, 1971; 2, Bird Rock, common, 1971.
Acanthina spirata (Blainville, 1832)
On rocks, mid-tide. 1, 2, common; 3, Jetty at Ocean Beach, common, 1971; 4, abundant, 1971.
Thais emarginata (Deshayes, 1839)
On rocks, high to mid-tide. 1, rocks north of Scripps Pier, occasional, 1970; 3, Jetty at Ocean Beach, common, 1971.

Buccinidae

Kelletia kelletii (Forbes, 1852)
On rocks or sand, low tide to subtidal. 2, La Jolla Cove, rare, 1971; 4, occasional, 1971, JCH; 5, off Point Loma at 18 m depth, 1970, JNM; 6, Shelter Island, occasional, 1971, JCH.
Macron lividus (A. Adams, 1855)
On or under small rocks in sand, mid- to low tide. 2, common, 1971; 5, Point Loma, common, 1971.

Columbellidae

Aesopus sanctus Dall, 1919 [see Keen, 1971]
2, La Jolla Cove, dead shells only, 1971.
Aesopus subturrita (Carpenter, 1864)
2, Camino de la Costa Beach, dead shells only, 1971.
Amphissa versicolor Dall, 1871
Under rocks, low tide to subtidal. 2, La Jolla Cove, occasional, 1967, FBG; 4, Ventura Point, occasional, 1971; 5, off Point Loma, on rocks at 18 m depth, common, 1970, JNM.
Nassarina penicillata (Carpenter, 1864)
In gravel and under rocks, low tide. 2, Beach and Tennis Club, occasional, 1971; 5, Point Loma, occasional, 1968, FBG
Mitrella carinata (Hinds, 1844)
On plants and rocks and in gravel, low tide. 2, common, 1971; 4, common on *Zostera,* 1971; 5, common, 1971.

Nassariidae

Nassarius fossatus (Gould, 1849)
In sand or mud, low tide to subtidal. 4, Vacation Isle, occasional, 1971; Flood Control Channel, abundant, 1971; 6, Shelter Island, occasional, 1971.
Nassarius mendicus (Gould, 1849)
In sand or mud, subtidal. 2, Windansea Beach, rare, 1967, FBG; 4, Flood Control Channel, common, 1971; 5, Point Loma, rare, 1970, JNM.
Nassarius perpinguis (Hinds, 1844)
In sand or mud, subtidal 1, Scripps Canyon, common, 1970, JNM; 4, Flood Control Channel, common, 1971.
Nassarius tegula (Reeve, 1853)
In sand or mud, low tide. 4, abundant, 1971; 6, Shelter Island, abundant, 1971.

Fusinidae

Fusinus luteopictus (Dall, 1871)
3, Tourmaline Surfing Beach, dead shell only, 1971.

Mitridae

Mitra idae Melvill, 1893
On rocks, low tide to subtidal. 2, Windansea Beach, rare, 1971, JCH; 4, Entrance Channel at 3 m depth, rare, 1970, JCH.

Marginellidae

Volvarina taeniolata Mörch, 1860
Under rocks, low tide. 2, 4, 5, common, 1971.
Cystiscus jewetti (Carpenter, 1857)
5, Point Loma at low tide, rare, 1968, FBG.
Cystiscus politulus (Dall, 1919)
2, La Jolla Cove, dead shells only, 1971.
1971.
Granula subtrigona (Carpenter, 1864)
Amongst algae, low tide. 2, Beach and Tennis Club, rare,
Granulina margaritula (Carpenter, 1857)
On *Zostera* blades, subtidal. 4, Flood Control Channel, common, 1971.

Olividae

Olivella baetica Carpenter, 1864
In sand, low tide to subtidal. 2, Beach and Tennis Club, occasional, 1967, JCH; 4, Flood Control Channel, common, 1971; 6, Shelter Island, common, 1967, JCH.
Olivella biplicata (Sowerby, 1825)
In sand, low tide to subtidal. 2, common, 1971; 4, abundant, 1971; 6, occasional, 1971.

Cancellariidae

Cancellaria cooperi Gabb, 1865
3, Tourmaline Surfing Beach, dead shells only, 1971.

Conidae

Conus californicus Hinds, 1844
In sand, often amongst rocks, low tide to subtidal. 2, common, 1971; 4, Flood Control Channel, common, 1971; 5, Point Loma, common, 1971.

Turridae

Megasurcula stearnsiana (Raymond, 1906)
In sand amongst rocks, at 18 m depth. 5, off Point Loma, rare, 1970, JNM.
Pseudomelatoma penicillata (Carpenter, 1864)
In sand or under rocks, low tide. 2, common, 1971; 5, Point Loma, common, 1970, FBG.

Mitromorpha aspera (Carpenter, 1864)
In gravel, low tide. 2, Bird Rock, rare, 1969, FBG.
Mitromorpha carpenteri Glibert, 1954
Under rocks, low tide. 3, Bird Rock, common, 1971.
Mitromorpha gracilior (Tryon, 1884)
2, Camino de la Costa Beach, dead shells only, 1971.
Crassispira semiinflata (Grant & Gale, 1931)
In sand, at 15 m depth. 5, off Point Loma, rare, 1970, JNM.
Ophiodermella ophioderma (Dall, 1908)
In sand, low tide. 2, Beach and Tennis Club, occasional, 1971; 4, Vacation Isle, occasional, 1971.
Clathromangelia fuscoligata (Dall, 1871)
2, La Jolla Cove, dead shells only, 1971.
Clathromangelia interfossa (Carpenter, 1864)
2, Camino de la Costa Beach, dead shells only, 1971.
Tenaturris janira (Dall, 1919)
In gravel, low tide. 2, Beach and Tennis Club, rare, 1971.
Clathurella canfieldi (Dall, 1871)
In gravel, low tide. 2, Bird Rock, rare, 1966, FBG.
Bellaspira grippi (Dall, 1908) [see McLean & Poorman, 1970]
2, La Jolla Cove, dead shells only, 1971.

PROSPECT

It is hoped that the census will stimulate further recording to fill the many gaps, and that the coverage will be extended to other groups of molluscs by local workers. Records of common species are particularly valuable, as there is a tendency to make assumptions about their universal presence. The distribution of rare species is often better recorded. It is a knowledge of major patterns of distribution, rather than range extensions, which are important in biogeographical interpretations.

The increasing pressure of the large urban population on the sea shores of the San Diego region takes many forms. The delicate intertidal area may be damaged by the large numbers of people seeking recreation on the beaches. There are obvious and immediate changes taking place as a result of mechanical alterations to the coast-line. These eliminate the transitional habitats such as salt marshes. Organic wastes and other chemicals have less obvious effects, but may be equally devastating in the long term. A review of the area at this stage of its history will prove valuable in conjunction with past and future work in charting any changes in the fauna.

Intertidal collecting of many invertebrates is now illegal in California, and several of the stretches of shore included in this study are completely protected as reserves. However, it is hoped that serious amateur workers will not be discouraged from making observations and records of species. This will be particularly useful if the compilation of data can be centred at an appropriate institution.

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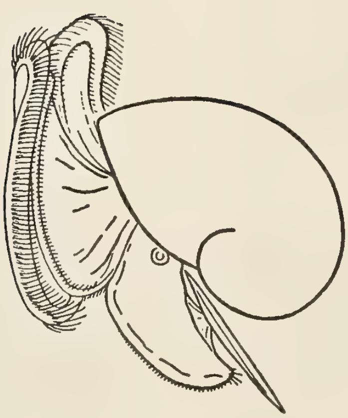

The Effect of Food Consumption on Growth, Fecundity, and Mortality in a Sacoglossan Opisthobranch, *Olea hansineensis*

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(2 Text figures)

INTRODUCTION

In order to understand the biology of any animal species it is important to know its feeding, which governs the success of the individual, and its reproduction, which governs the success of the species. Although a large number of studies has been published on either feeding or reproduction of marine invertebrates, little is known of the relationship between the two in one species. This is perhaps due to the difficulties in making direct measurements of both parameters simultaneously. *Olea hansineensis* Agersborg, 1923, proves ideal for such a study; it is small (7 mm long), short-lived (3 months), a carnivore (feeds on the eggs of other opisthobranchs) and readily lays eggs in culture dishes. Therefore, the feeding and reproduction of a large number of animals can be studied easily, in a relatively short period of time.

In this paper we report laboratory observations on the effect of the amount and kind of food on growth, fecundity and mortality.

MATERIALS AND METHODS

On June 4, 1970, 20 *Aglaja diomedea* (Bergh, 1894) (hereafter referred to as *Aglaja*) egg masses were collected subtidally (12 m) from the bay immediately south of the Friday Harbor laboratories. From these, 60 young *Olea* (1 mm in length) were removed. Twenty of these were placed in each of 3 fingerbowls (A, B, and C). The fingerbowls were kept in sea water tables at a temperature of 10 - 15° C. The water in the bowls was changed every 2 to 3 days.

The *Olea* in the 3 bowls were treated as follows: Those in bowl A were fed *Aglaja* eggs throughout the entire course of the experiment; those in bowl B were fed *Archidoris montereyensis* (Cooper, 1862) (hereafter referred to as *Archidoris*) eggs for the first week, but as they showed little appetite for these, were changed to *Haminoea virescens* (Sowerby, 1833) (hereafter referred to as *Haminoea*) eggs, a strongly preferred food (Crane, 1969, 1971), and animals in bowl C were starved for the first week, and then fed *Aglaja* eggs for the remainder of the experiment. These conditions simulate some variables of natural feeding conditions: some animals may feed continuously on a preferred food (A), others may first feed on a less preferred food and then change to a strongly preferred one (B), and still others may be unable to find food for a short period (C).

All bowls were supplied with an excess of food so that the *Olea* always had the option of feeding. The amount of food (number of eggs) consumed was determined by subtracting the estimated number of uneaten eggs in an egg mass from the number of eggs originally estimated in the mass.

Length measurements of *Olea* were taken once a week, with the aid of a dissecting microscope. They were measured from the anterior margin of the oral lobes to the tip of the foot when naturally distended and moving along the bottom of a petri dish.

Once sexual maturity was reached, the *Olea* began to lay spiral egg masses (almost exclusively on the glass wall of the bowl). These were removed daily, and the number of spawn masses and the number of eggs per spawn mass were recorded.

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The experiment extended from June 4 to August 26, 1970. At the time of termination, both feeding and reproductive activity had declined to very low levels and many *Olea* had died. Therefore, the surviving *Olea* were considered to be very close to the end of their life spans.

Food Consumption:

For each of the bowls, the average amount of food consumed per *Olea* within each time interval, in most cases, one week, is presented in Table 1. Since the eggs of *Aglaja* and *Haminoea* are spherical in shape, the volume was calculated from the diameter. The diameter of *Aglaja* eggs is 90 μm and of *Haminoea* eggs is 94 μm. Since only a small number (600) of *Archidoris* eggs was consumed in bowl B, the volume of *Archidoris* eggs was taken as the same as that of *Haminoea*.

As shown in Table 1, the total volume of eggs consumed by an individual *Olea* during the 80-day study period is approximately the same in bowls A and C, but the amount consumed by an individual in bowl B is more than twice as much. This difference will be noted again in connection with growth and fecundity.

Growth:

Based on the size of the advanced veliger and on the subsequent growth rate which we have observed, the time required for an *Olea* to attain 1 mm after metamorphosis is estimated to be 5 days. From 1 mm, *Olea* grow rapidly and reach sexual maturity in 2 to 3 weeks, depending on the feeding conditions. They spawn many times in the remaining span of their lives.

Olea of 1 mm are white and have no cerata or, sometimes, the buds of the first two. By the time they are 2 mm, the grey color pattern and the first 2 cerata have developed. There is a positive correlation between the number of cerata and the size of the animal. The largest *Olea* observed in the laboratory measured 13 mm, and this individual had 8 major and 8 minor cerata. The largest *Olea* found in the field during biweekly collections throughout the summer, 1970, was only 8 mm in length.

Table 2 shows the growth, egg production, and mortality of *Olea* in the 3 bowls recorded at weekly intervals. The growth is again represented in Figure 1, which resembles a sigmoid curve. It is noted from Figure 1 that *Olea* in bowl A had the greatest initial rate of growth.

Table 1

Food Consumption by Animals in Three Experimental Conditions throughout the 80-Day Study Period

	Bowl A		Bowl B		Bowl C	
Date (1971)	Average no. of eggs consumed per *Olea*	Volume (ml) of eggs consumed per *Olea*	Average no. of eggs consumed per *Olea*	Volume (ml) of eggs consumed per *Olea*	Average no. of eggs consumed per *Olea*	Volume (ml) of eggs consumed per *Olea*
Jun 4 - 10	5 250	2.01	600	0.26		
Jun 11 - 17	6 200	2.37	5 750	2.50	4 000	1.53
Jun 18 - 26	12 550	4.79	5 150	2.24	11 200	4.28
Jun 27 - Jul 5	13 150	5.02	13 600	5.92	7 600	2.90
Jul 6 - 12	3 400	1.30	8 050	3.50	5 600	2.14
Jul 13 - 19	5 250	2.01	11 600	5.04	8 350	3.19
Jul 20 - 26	2 450	0.94	20 200	8.78	6 450	2.46
Jul 27 - Aug 2	4 500	1.72	21 050	9.16	8 550	3.27
Aug 3 - 9	2 250	0.86	17 050	7.42	2 600	0.99
Aug 10 - 16	2 600	0.99	9 850	4.28	3 750	1.43
Aug 17 - 23	700	0.27	10 700	4.65	1 200	0.46
Totals	58 300	22.28	123 600	53.75	59 300	22.65

Volume of one *Aglaja* egg = 0.000 382 ml
Volume of one *Haminoea* egg = 0.000 435 ml

Table 2

Growth, Egg Production, and Mortality during the 80-Day Study Period

Date (1971)	Bowl A: Number of *Olea*	Bowl A: Mean length (mm)	Bowl A: Average no. of eggs per day per *Olea*	Bowl B: Number of *Olea*	Bowl B: Mean length (mm)	Bowl B: Average no. of eggs per day per *Olea*	Bowl C: Number of *Olea*	Bowl C: Mean length (mm)	Bowl C: Average no. of eggs per day per *Olea*
Jun 4	20	1.0	0	20	1.0	0	20	1.0	0
Jun 11	20	2.4	0	19	1.9	0	15	1.5	0
Jun 18	20	4.3	9	19	3.8	0	15	3.0	0
Jun 27	20	6.1	126	18	5.7	96	15	5.5	8
Jul 6	20	6.7	329	18	7.1	508	15	7.3	37
Jul 13	20	7.0	202	18	7.8	368	14	7.1	176
Jul 20	20	7.1	157	16	8.0	450	14	7.3	121
Jul 27	20	6.5	89	16	8.3	261	14	6.8	53
Aug 3	20	6.3	106	16	8.5	376	13	6.6	35
Aug 10	20	6.2	34	14	8.6	366	12	6.8	19
Aug 17	20	5.5	48	13	7.3	280	12	6.2	92
Aug 24	18	5.4	3	10	7.6	142	8	5.7	18

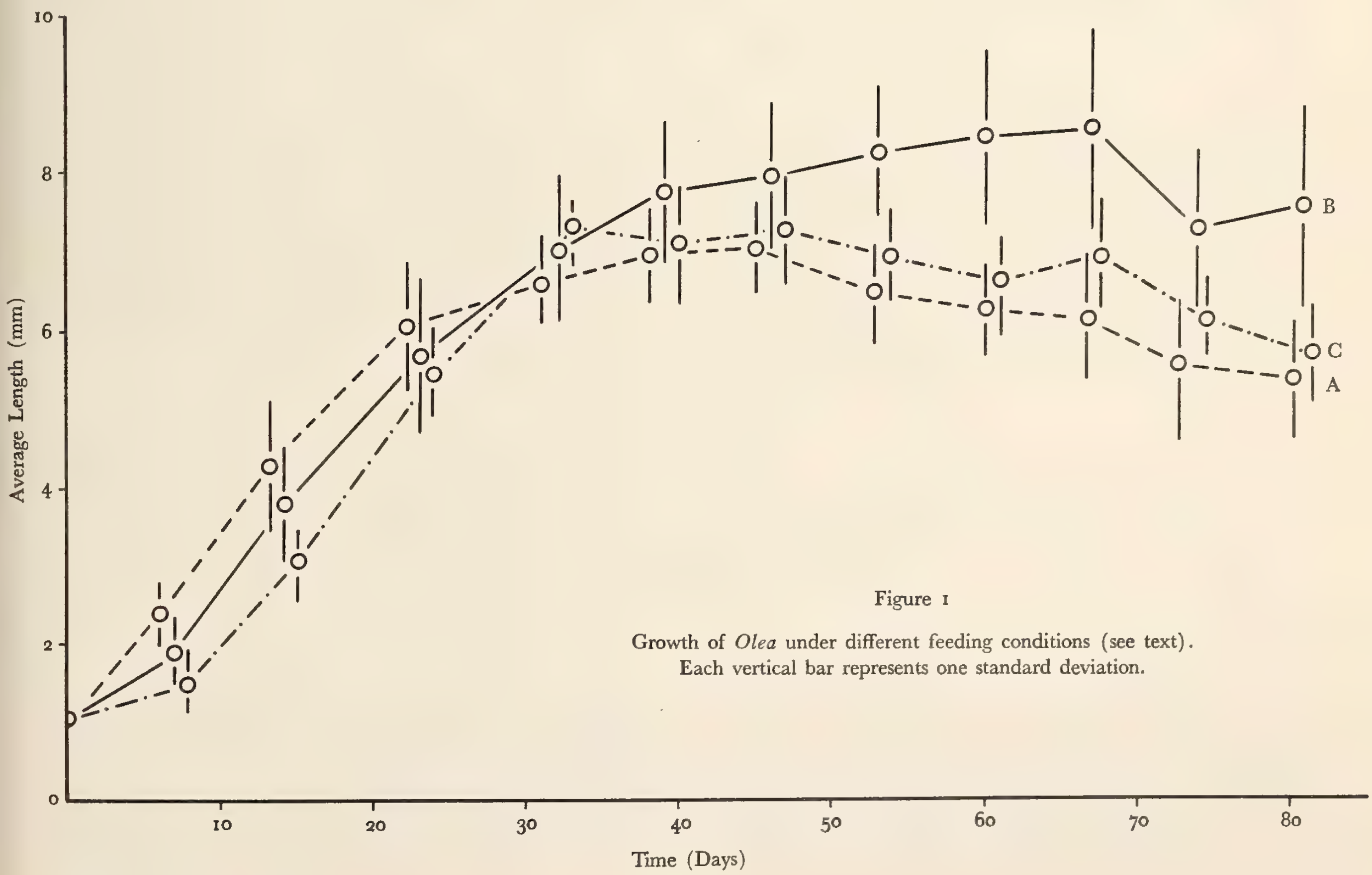

Figure 1

Growth of *Olea* under different feeding conditions (see text). Each vertical bar represents one standard deviation.

These *Olea* also had the most preferred feeding conditions during the first week (*Aglaja* embryos as opposed to *Archidoris* in bowl B, and starvation in bowl C). Although the *Olea* of bowl C were starved during the first week, their growth was not permanently impaired. After about 20 days of feeding on the same diet, their size does not differ significantly ($P < 0.95$) from that of *Olea* in bowl A. Because, after a 6-week period, the size of *Olea* in bowl B deviates significantly ($P > 0.999$) from those in bowls A and C, the type of food appears to be most important in growth.

The body of *Olea* has no rigid supporting structures, so its size is quite flexible. For example, the July 13 dip in average size of *Olea* in bowl C corresponds to the week of peak spawning, indicating that the emptying of gonads resulted in shrinkage of the body.

Average maximum size in bowl A (7.1 mm) was attained in the 7th week; this was followed by a gradual decline. In bowl B, the same size was reached in the 5th week, but growth continued, and an average maximum size of 8.6 mm was reached in the 10th week. Although *Olea* in bowl C were starved during the first week, the average maximum size of 7.3 mm was reached in the 5th week.

Mortality:

Nourishment during the first week did have some effect on longevity. As is shown in Table 2, after 12 weeks 18 *Olea* in bowl A were still alive. In contrast to this, 5 of the 20 *Olea* in bowl C died during the week of starvation, the others all lived for the next 26 days, and then gradually began to die until only 8 remained after 12 weeks. Although those of bowl B were not starved, deaths occurred gradually and regularly which is likely due to the feeding on less preferred food during the first week.

Fecundity:

The *Olea* in bowl A began to lay eggs at an average length of 4.3 mm, and in bowls B and C at 4.2 mm. In bowl A, the egg laying began 14 days after the experiment began; in bowl B it began 2 days later; and, interestingly, in bowl C it was delayed one week, the same duration these *Olea* were initially starved.

Figure 2 shows the cumulative number of eggs laid per *Olea* with time. The 1-week starvation period of animals in bowl C does not delay their peak spawning day, but it appears to have a permanent effect on their fecundity. Although animals in this bowl were later fed *Aglaja* embryos as were those in bowl A, the total egg production per *Olea* continually remained below that of bowl A. In bowl B, the cumulative production initially lagged behind that in bowl A, probably due to the lower food consumption of *Archidoris* embryos during the first week. After 2 weeks of spawning, cumulative egg production of the *Olea* in bowl B surpassed that of bowl A and continued to rise steadily, whereas in bowl A it gradually levelled. When the food consumption is examined, unsurprisingly in bowl B it continued with egg production, and in bowl A it dropped (Table 1).

In bowl A, the average number of eggs in one *Olea* spawn mass was 435 the first month (of spawning) and 192 the second month; in bowl B it was 468 the first month and 444 the second; and in bowl C it was 325 the first month and 215 the second. Therefore, the average spawn masses laid in the first month contained more eggs than an average one laid in the second.

The total egg production during *Olea*'s reproducing life of approximately 2 months was: in bowl A, 8 546 eggs or 2.29 ml; in bowl B, 20 836 eggs or 5.58 ml; and in bowl C, 7 037 eggs or 1.89 ml. Since all other environmental conditions were comparable in the 3 bowls, the dramatic difference in egg production can be attributed either to the quality, or quantity, or both, of the food the *Olea* consumed.

CONCLUSION AND DISCUSSION

In order to appreciate the data fully, the 3 interdependent factors: food consumption, growth, and fecundity must be considered simultaneously. A summary of the results is given in Table 3. From this table it is noted that the total volume of food consumed by an individual *Olea* in bowls A and C is approximately equal (1 : 1.01). Also, there is no significant difference ($P > 0.05$) in the maximum av-

Table 3

Summary of Growth, Food Consumption, Egg Production and Percentage of Egg Production of Food Consumed

	Bowl A	Bowl B	Bowl C
Average maximum size attained (mm)	7.1	8.6	7.3
Total food (ml) consumed per *Olea*	22.28	53.75	22.65
Total number of eggs laid per *Olea*	8 546	20 836	7 037
Total volume (ml) of eggs laid per *Olea*	2.29	5.58	1.89
% (by volume) eggs laid of food consumed	10.3	10.4	8.3

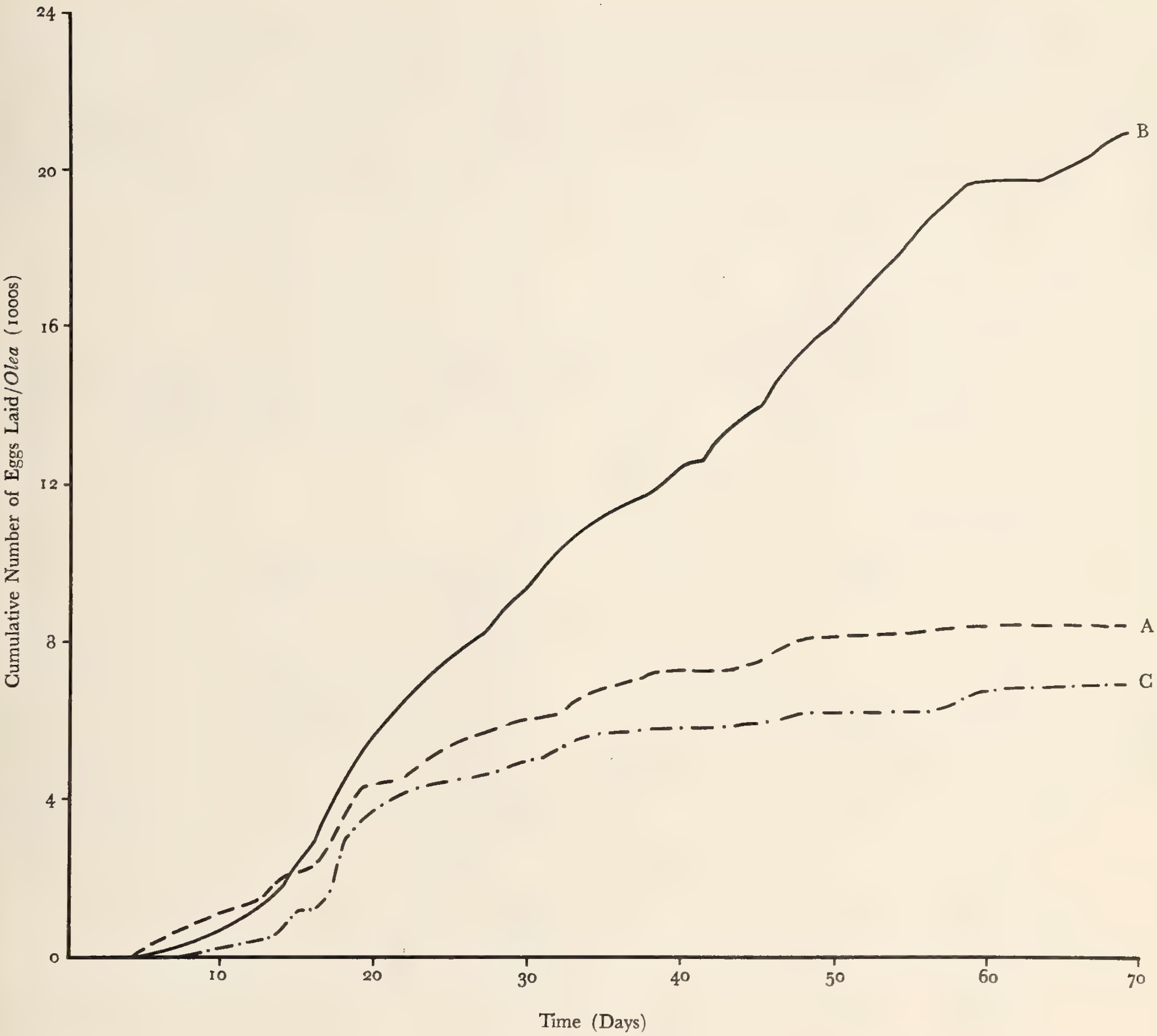

Figure 2

Cumulative number of eggs produced by each *Olea* in three bowls during a period of 80 days.

erage size attained in these two bowls. However, the total number of eggs laid per *Olea* in bowl A is 1.21 times as great as in bowl C; the fecundity of those in bowl C was likely impaired due to the initial week of starvation. It is interesting that starvation during the juvenile stage did not retard growth, but did negatively affect the longevity and fecundity.

The greater number of eggs laid in Bowl B than in bowl A can be explained in terms of food consumption. In bowl A, food consumption dropped immediately after the peak spawning period, whereas, in bowl B, the *Olea* continued to feed and to lay eggs at a steady rate. An *Olea* in bowl B laid 2.44 times as many eggs as did one in bowl A, and, correspondingly, consumed 2.41 times as much

food. As well as having greater fecundity, the maximum average growth attained in bowl B was significantly greater than in bowl A ($P > 0.999$).

The results indicate that a fixed volume of *Haminoea* eggs yields to an *Olea* more utilizable energy than does an equal volume of *Aglaja* eggs. The volume of eggs produced was 10.3% and 10.4% of the volume of food consumed in bowls A and B respectively, but the *Olea* in bowl B grew 1.21 times larger than those in bowl A. Differences in quality between eggs (embryos) of *Haminoea* and *Aglaja* probably explain why the *Haminoea*-fed *Olea* (bowl B) continued to feed and to reproduce, following the peak spawning period, while in *Aglaja*-fed Olea (bowls A and C) both of these activities declined.

It should be noted that during the first 3 weeks most of the energy consumed was directed toward growth. At the end of this period, the *Olea* had attained an average size of 0.7 mm (bowl A: 6.7 mm; bowl B: 7.1 mm; bowl C: 7.3 mm). Immediately after 3 weeks, energy directed towards growth dropped sharply. During the 4th week (5th in bowl C) spawning showed a sharp increase, and from then on the majority of the energy was directed towards this activity.

The egg production in *Olea* is much higher than that of other sacoglossan opisthobranchs which have been studied. For example, *Olea* in bowl A produced 10 times more eggs than *Limapontia capitata* (Müller, 1773) and 20 times more than *Acteonia cocksi* Alder & Hancock, 1862 (Chia, 1971). Although both *Limapontia* and *Acteonia* are slightly smaller than *Olea* and lived and reproduced for only about 40 days in the laboratory, the differences in fecundity are still considerable. These differences are perhaps related to the kinds of foods the animals consume; *Olea* is carnivorous while the other sacoglossans feed on algae. Also, one would assume that, at metamorphosis, the chances for an *Olea* larva finding an opisthobranch egg mass are much less than for a *Limapontia* or *Acteonia* larva finding some algae. Therefore, higher larval mortality would necessitate greater fecundity of *Olea*.

ACKNOWLEDGMENTS

This research was supported by a grant from the National Research Council to F. S. Chia. We thank Dr. R. L. Fernald, Director of the Friday Harbor Laboratories, University of Washington, for providing facilities.

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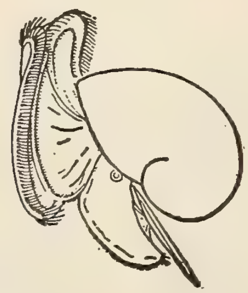

Late Pleistocene Marine Invertebrates from Rancho Miramar and Las Cruces, Southern Baja California del Sur

BY

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(1 Text figure)

INTRODUCTION

INVERTEBRATE FOSSIL FAUNAS contained in Pleistocene terrace deposits are fairly well documented in parts of Baja California (JORDAN, 1924, 1936; HERTLEIN, 1934; DURHAM, 1950; CHACE, 1956; EMERSON, 1960; EMERSON & HERTLEIN, 1964), but data pertaining to these faunas in the Cape region of the Peninsula are relatively sparse. HERTLEIN (1957) reported small Pleistocene invertebrate faunas collected by E. T. Hammond in the El Coyote, Rancho Miramar, and Buena Vista areas in the region south of La Paz, and SQUIRES (1959) has reported similar faunas in the Cabo Pulmo area and from the south side of Isla Cerralvo. EMERSON (1960), and EMERSON & HERTLEIN (1964), subsequently reported small late Pleistocene invertebrate faunas from the south and west sides of Isla Cerralvo, respectively (Figure 1). To our knowledge, there are no records of Pleistocene invertebrate faunas on the Pacific side of Baja California south of the Bahía Magdalena localities of JORDAN (1936).

In this study we are reporting 21 invertebrate taxa in addition to the 6 species previously reported by HERTLEIN (1957: 59) from Hammond's Rancho Miramar locality, and 27 invertebrate taxa from a previously unreported locality at Las Cruces, 25 km north of Rancho Miramar (Figure 1; Table 1). These 2 areas are included in a coastline study we completed in February, 1972 between La

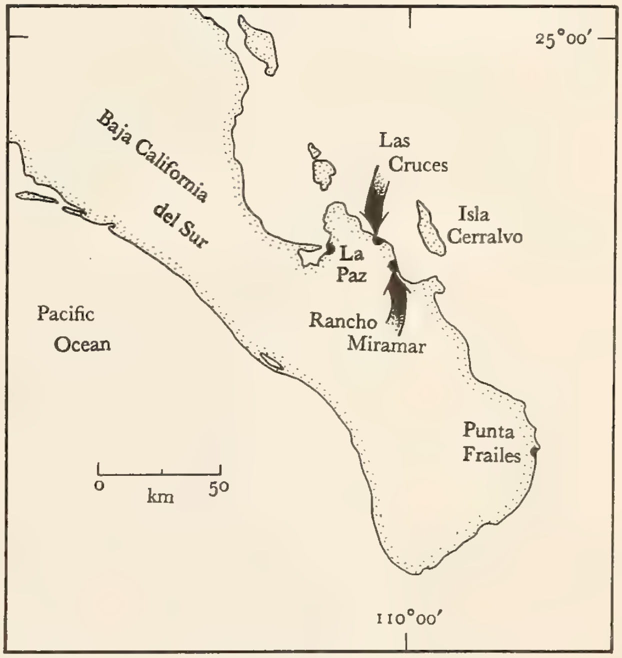

Figure 1

Index Map of Southern Baja California del Sur (indicating areas mentioned in the text)

Table 1

FAUNAL LIST[1]

MOLLUSCA	Las Cruces	Rancho Miramar
Bivalvia	(SDSNH 0434)	(SDSNH 0435)
Arca (Arca) pacifica (Sowerby, 1833)		×
Glycymeris (Glycymeris) gigantea (Reeve, 1843)		×*
Glycymeris (Glycymeris) maculata (Broderip, 1832)		×*
Pinctada mazatlanica (Hanley, 1856)	×	×*
Ostrea (Lopha) megodon Hanley, 1846		×
Pecten (Oppenheimopecten) vogdesi Arnold, 1906		×
Lyropecten (Nodipecten) subnodosus (Sowerby, 1835)		×
Spondylus calcifer Carpenter, 1857		×
Lucina (Callucina) lampra (Dall, 1901)	×	
Chama echinata Broderip, 1835		×
Chama mexicana Carpenter, 1857	×	×
Chione (Chione) californiensis (Broderip, 1835)		×*
Chione (?Chione) tumens (Verrill, 1870)	×	
Protothaca (Tropithaca) grata (Say, 1831)		×
Protothaca sp.	×	
Gastropoda		
Turbo (Callopoma) fluctuosus Wood, 1828	×	×*
Nerita scabricosta Lamarck, 1822	×	
? *Dendropoma* sp.	×	
Cerithium (Thericium) maculosum Kiener, 1841	×	×*
Strombus (Strombus) gracilior Sowerby, 1825		×
Strombus (Lentigo) granulatus Swainson, 1822	×	
Strombus (Tricornis) galeatus Swainson, 1823		×
Strombus cf. *S. (T.) galeatus* Swainson, 1823	×	
Hipponix pilosus (Deshayes, 1832)	×	
Crucibulum (Crucibulum) scutellatum (Wood, 1828)		×
Polinices (Polinices) uber (Valenciennes, 1832)	×	
Polinices (Neverita) recluzianus (Deshayes, 1839)	×	
Cypraea (Zonaria) annettae Dall, 1909	×	×
Hexaplex sp.	×	
Thais (Mancinella) speciosa (Valenciennes, 1832)		×
Neorapana muricata (Broderip, 1832)	×	×
Columbella aureomexicana (Howard, 1963)	×	
Fasciolaria (Pleuroploca) princeps Sowerby, 1825		×
Fusinus (Fusinus) dupetitthouarsi (Kiener, 1840)	×	
Olivella (Olivella) dama (Wood, 1828, *ex* Mawe, MS)	×	
Mitra (Strigatella) tristis Broderip, 1836	×	
Cancellaria sp.	×	
Conus (Conus) brunneus Wood, 1828	×	×
Conus cf. *C. (C.) princeps* Linnaeus, 1758	×	
Conus cf. *C. (Leptoconus) regularis* Sowerby, 1833		×
Conus (Ximeniconus) ximenes Gray, 1839	×	
Polyplacophora		
Chiton sp.		×
ANTHOZOA		
Porites californica Verrill, 1870	×	×
Pocillopora elegans Dana, 1846	×	×
ARTHROPODA		
Balanus cf. *B. trigonis* Darwin, 1854		×

[1] Taxa marked with an asterisk were also reported by HERTLEIN, 1957

Paz and Punta Frailes, via a helicopter generously provided by the Consejo de Recursos Naturales no Renovables in Mexico City.

GEOLOGIC SETTING

The coastline between Las Cruces and Rancho Miramar is devoid of emergent Pleistocene terraces, with the exception of a few, small, isolated benches cut into a rugged, granitic coastline.

At Las Cruces, the marine terrace is approximately 6m in elevation, 2km in length, and is bounded by granitic headlands. Fossils were found at only one exposure, in a sea cliff 3m above sea level [San Diego Society of Natural History (SDSNH) Locality 0434]. This locality is along an unpaved road leading from La Paz to Las Cruces, and is approximately 1km north of the resort. The fossils are contained in an extremely poorly-sorted boulder conglomerate, and are in general water worn, leached, and poorly preserved.

At Rancho Miramar, the marine terrace is approximately 12m in elevation, and forms part of a large terrace exposure bordering Bahía Ventana. Well preserved fossils were collected in a poorly-sorted, cobble sized, alluvial fanglomerate (SDSNH Locality 0435) 7m above sea level, along a 200m stretch of beach at the Hammond locality (Hertlein, 1957: 59). Travel to this locality and the one at Las Cruces is possible by automobile from La Paz; rugged topography and the lack of a road presently makes coastal travel between the localities impossible by automobile.

GEOLOGIC AGE

A late Pleistocene age is assigned to both localities due to their presence on the lowest emerged terrace in the region, and the fact that living representatives of the species collected presently occur in the adjacent coastal waters. This evidence further refines the "Pleistocene" age assignment given the Rancho Miramar locality by Hertlein (1957: 59, 60).

FAUNAL CONSIDERATIONS

Due to the relatively small number of taxa collected, only general paleoenvironmental conclusions concerning the 2 faunas can be made.

At Las Cruces, depth of burial is suggested by faunal and field evidence to have been in shallow water slightly deeper than the intertidal zone. Only one species, *Nerita scabricosta,* was collected that is presently confined to the intertidal zone, while the rest of the fauna presently ranges in waters including, or slightly deeper than, the intertidal zone, to much deeper depths (Keen, 1971). Field evidence delineates the late Pleistocene shoreline angle in this region to be approximately 150m inland from the fossil locality, at a point where the terrace sediments abut the high-relief granitic basement complex.

Transport prior to burial is indicated by the association of *Nerita scabricostata,* a high-intertidal zone species, with *Lyropecten (Nodipecten) subnodosus, Pinctada mazatlanica,* and *Mitra (Strigatella) tristis,* species presently restricted to depths greater than the intertidal zone (Keen, 1971). Only one species, *Lucina (Callucina) lampra,* was collected with both valves paired, suggesting *in situ* burial in the cobble and boulder substrate. Agitation prior to burial is also indicated by the water-worn and fragmented condition of the fauna.

At Rancho Miramar, faunal evidence suggests the depth of burial to be in, or slightly deeper than, the intertidal zone. Only 4 taxa, *Chama echinata, Turbo (Callopoma) fluctuosus, Strombus (Tricornis) galeatus,* and *Thais (Mancinella) speciosa,* were collected that are presently restricted to the intertidal zone. The remaining taxa presently range in waters including, or slightly deeper than, the intertidal zone, to much deeper depths (Keen, 1971). The fossils were contained in an angular, alluvial sediment exhibiting little or no sign of current abrasion.

A relative lack of transport prior to burial in the alluvial substrate is indicated by relatively unworn and unbroken valves of *Pinctada mazatlanica, Glycymeris (Glycymeris) maculata,* and *Pecten (Oppenheimopecten) vogdesi,* the most common mollusks present, and 2 intact individuals of *Fasciolaria (Pleuroploca) princeps,* averaging 110cm in altitude.

The presence of only one fossiliferous deposit in the 3km alluvial seacliff studied at Rancho Miramar suggests that paleo-current regimes in the adjacent coastal waters have, during Recent time, extensively eroded a once much more widespread marine coastal terrace. This, in turn, suggests that the fossil locality may represent only a remnant embayment in this terrace. This hypothesis is supported by the angular and poorly-sorted alluvial composition of the seacliff sediments, and the virtual lack of water-worn cobbles in the sediments. The alluvial composition of the seacliff was also noted by Hammond (in Hertlein, 1957: 59).

There is no faunal indication at either locality suggesting that the late Pleistocene water temperature was different than that which exists in the Gulf of California today.

ACKNOWLEDGMENTS

We wish to thank the Consejo de Recursos Naturales no Renovables and their representative Francisco Altamirano for use of the helicopter. R. Gordon Gastil, Department of Geology, California State University, San Diego, supplied financial support under his NSF Grant. Arnold Ross, Curator of Paleontology, San Diego Natural History Museum, provisionally identified the cirriped, and George Radwin, Curator of Invertebrate Zoology, San Diego Natural History Museum, kindly made available the museum's Recent molluscan collections during this study. The fossils are on deposit at the San Diego Natural History Museum.

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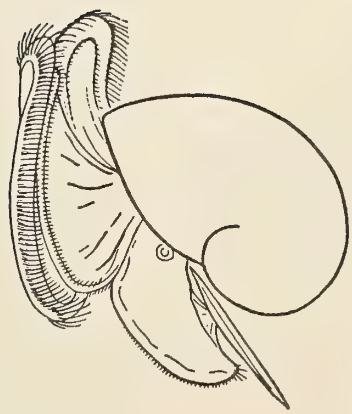

Observations on Feeding and Prey Specificity of *Tritonia festiva* (Stearns) with Comments on other Tritoniids

(Mollusca : Opisthobranchia)

BY

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(1 Plate)

Tritonia festiva (Stearns, 1873) has been reported to occur from the Coronados Islands, Mexico to Vancouver Island, Canada (LANCE, 1961) and also in Japan (THOMPSON, 1971). On numerous occasions I have encountered this species off La Jolla, California, principally at about 30m depth on the north rim of the Scripps Branch of the La Jolla submarine canyon and at 20m depth on an artificial reef about 1.6km to the north. On almost every occasion I have found the nudibranch on the pink gorgonian, *Lophogorgia chilensis* (Verrill, 1868) (see Plate).

My research on the barnacle *Balanus galeatus* (Linnaeus, 1771), which is commensal on gorgonians (MOLENOCK & GOMEZ, 1972) led me to investigate the role that the nudibranch might play in the ecology of the cirriped. The cyprid larva of the barnacle attaches itself on the exposed axial skeleton of the gorgonian. Since some nudibranchs are known predators of alcyonarians (THOMPSON, 1964,), I set out to determine if *Tritonia festiva* fed on *Lophogorgia*.

On one occasion I brought back to the laboratory 2 specimens of the nudibranch. On examination I observed the gut to appear deep pink through the translucent body. Upon dissection the gut yielded spicules of the coelenterate. Subsequently, the fecal pellets of the second specimen also yielded spicules. Here was direct evidence that *Tritonia festiva* fed on *Lophogorgia chilensis*.

I was next interested to verify if the nudibranch actually exposed the axis of the gorgonian in its feeding or whether it merely browsed the surface of the coenenchyme. I subsequently brought up from the field some gorgonian branches and several other nudibranchs and placed them on the laboratory sea table.

On the next day I observed one nudibranch 30mm long crawling on an upraised branch of *Lophogorgia*, seeming to feel its way with its cephalic tentacles. It continued distally until it reached the branch termination, whereupon it spread the oral veil over the tip which became engulfed within the pharynx. With a single bite, a 2mm length of the tip was trimmed off. It passed this piece into its stomach and appeared to rest for a few minutes, after which the oral veil was again placed over the cut tip. This time the nudibranch was not able to break off the entire tip since the gorgonian axis is stouter here. Half the "rind" of the branch was stripped, leaving about 2mm of the axial skeleton exposed. When the feeding process was over half an hour later, about 4mm of the axis of the gorgonian had been denuded of coenenchyme.

I observed one other *Tritonia* feed on *Lophogorgia* in the laboratory. Although I have not actually witnessed this feeding process in the field, I have on numerous occasions seen exposed axes on branch tips of the gorgonian. There is little doubt that some of these were feeding sites of the nudibranch. It is on these denuded tips that settling cyprid larvae attach, as borne out by the fact that more often than not, adult barnacles on *Lophogorgia* are located terminally on the branches. Along with other physical and biological agents, *Tritonia festiva* thus serves to prepare a substrate for the settlement of the barnacle on the gorgonian (see Plate).

Since gorgonians become scarce as one proceeds north along the coast, I was puzzled to learn that *Tritonia festiva* was not uncommon in Puget Sound. Either the reports were inaccurate or the nudibranch fed on other prey. A letter from Dr. Charles Birkeland, who had studied the predators of the sea pen *Ptilosarcus guerneyi* (Gray) in Washington (doctoral dissertation, University of Washington, 1970) provided me with the answer. I learned that *T. festiva* feeds on this sea pen in Puget Sound.

This nudibranch is not therefore limited to a single prey species. A parallel case is that of *Tritonia plebeia* (Johnston, 1828). THOMPSON (1964) lists its diet to include the alcyonacean *Alcyonium digitatum* and the gorgonian

Eunicella verrucosa. A recent paper (Wicksten & DeMartini, 1973) reports that the tritoniid *Tochuina tetraquetra* (Pallas, 1788) feeds on *Gersemia rubiformis* in Trinidad Bay, California. As no mention is made of other prey species, one might conclude that it feeds exclusively on *Gersemia.* While this may be true for Trinidad Bay, Thompson (1971) mentions that it feeds on *Ptilosarcus* in Washington, while MacFarland (1966) had noted spicules, presumably gorgonian in origin, in the gut of *Tochuina.*

In the feeding experiments of Wicksten and DeMartini, they offered the nudibranch cnidarians that were found in its habitat (Wicksten, personal communication). I would like to note that the 3 species rejected by the tritoniid nudibranch were zoantharians or hexacorals. A survey of the literature reveals that the members of the family Tritoniidae prey almost exclusively on the subclass Alcyonaria (= Octocorallia). The data available are given in Table 1.

Thompson (1964), who reviews the diet of the British nudibranchs, has some reservations about hydroids being included among the prey of *Tritonia plebeia.* Whether oysters are actively sought by the large British nudibranch *T. hombergi* or whether they are ingested only incidentally is an interesting question. If they are digested when passed through the gut, they would represent the only known prey species outside the phylum Coelenterata. Indeed, the tritoniid nudibranchs appear to limit themselves to the alcyonarian orders Stolonifera, Alcyonacea, Gorgonacea, and Pennatulacea.

Data are accumulating indicating that species of the family Tritoniidae are not strictly prey specific, but that their diet varies from region to region. In a given locality, however, a population may be limited to a single prey species.

I thank Mr. James R. Lance and Dr. Gordon Robilliard for criticizing the manuscript.

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Table 1

Prey Species of the Tritoniidae

Predator	Prey	Source
Tritonia exsulans Bergh, 1894	Sea pen	Marcus, 1961
Tritonia hombergi Cuvier, 1803	*Alcyonium digitatum*;	Thompson, 1962
	oysters	Thompson, 1964
Duvaucelia odhneri Tardy, 1963	*Eunicella verrucosa* (Pallas)	Tardy, 1963
Tritonia lineata (Alder & Hancock, 1846)	Alcyonarians	Thompson, 1964
Tritonia plebeia (Johnston, 1838)	*A. digitatum, E. verrucosa,* hydroids	Thompson, 1964
Tochuina tetraquetra (Pallas, 1788)	Alcyonarian (*Euplexaura marki* ?)	MacFarland, 1966
	Ptilosarcus guerneyi	Thompson, 1971
	Gersemia rubiformis (Pallas)	Wicksten & DeMartini, 1973
Tritonia diomedea (Bergh, 1894)	*Virgularia* sp.	Thompson, 1971
Tritonia pickensi Marcus & Marcus, 1967	Gorgonian (implied)	Keen, 1971
Tritonia wellsi Marcus, 1961	*Leptogorgia virgulata* (Lamarck)	Patton, 1972
Tritonia bayeri Marcus & Marcus, 1967	*Briareum asbestinum*	Salvini-Plawen, 1972
	Pseudopterogorgia sp.	
Tritonia manicata Deshayes, 1839	*Cornularia* sp.	Salvini-Plawen, 1972
Tritonia striata Haefelfinger, 1963	*Paralcyonium elegans*	Salvini-Plawen, 1972
Tritonia festiva (Stearns, 1873)	*Ptilosarcus guerneyi* (Gray)	Birkeland, pers. comm.
	Lophogorgia chilensis (Verrill)	Gomez, personal observations

Figure *1*

Tritonia festiva on *Lophogorgia chilensis*

The nudibranch is attached to a branch on which it has just fed. Note injured branch tip and exposed axis of the gorgonian at top center. Gall-like expansions on the gorgonian at center background and at extreme left branch terminus are the barnacle, *Balanus galeatus*. White polyps of the gorgonian are expanded at left, retracted elsewhere. Underwater Kodachrome (from which this black-and-white print was made) through the courtesy of Chuck Nicklin, Diving Locker, San Diego.

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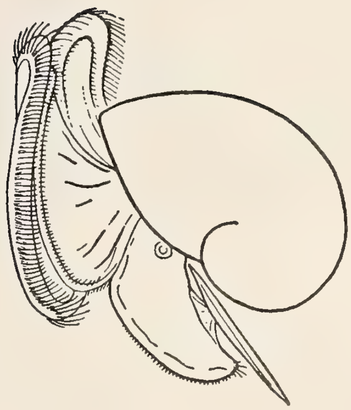

Fine Structure of the Eye of the Prosobranch Mollusk *Littorina scutulata*

BY

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(5 Plates)

INTRODUCTION

THE EYE, SITUATED on the ocular bulge at the base of each of the two tentacles on the head of the winkle, *Littorina littorea* Linnaeus, 1758 was described by NEWELL (1965) using light microscopy. CHARLES (1966), citing an unpublished electron microscopic study by Owen & Charles, provided additional information on the fine structure of these eyes.

The eyes at the tips of the posterior tentacles on the head of the garden snail *Helix aspersa* Müller, 1774, have been more completely described by BRANDENBURGER & EAKIN (1970) and EAKIN & BRANDENBURGER (1967a, 1967b, 1967c).

The present study describes the fine structure of the eyes of another littorine, *Littorina scutulata*, and compares these structures to those of *L. littorea* and *Helix aspersa*.

MATERIALS AND METHODS

Specimens of *Littorina scutulata* Gould, 1848, were collected intertidally at Bodega Head on the northern California coast.

The eyes of these snails were removed and fixed for 1 hr at room temperature in 4% glutaraldehyde and 0.15M, pH 7.3 sodium cacodylate buffer in 0.15M sodium chloride, washed for 30 minutes in 0.15M sodium cacodylate buffer and 0.15M sodium chloride, and postfixed for 1 hr in ice cold 2% OsO_4 in 0.15M sodium cacodylate buffer and 0.15M sodium chloride. Dehydration in ethanol and propylene oxide was followed by Epon embedding.

One μm thick sections were mounted on glass slides and stained with 1% toluidine blue in 1% borax for light microscopy.

Silver ultrathin sections were mounted on coated grids and stained for 30 minutes in uranyl acetate and 5 minutes in lead citrate. Electron micrographs were taken with a Zeiss EM 9A.

RESULTS

Each of the two eyes of *Littorina scutulata* is located in an ocular bulge at the base of a tentacle. Covering each is a transparent skin (cornea) composed of columnar epithelial cells bearing microvilli at their tips. The eye, encapsulated by dense connective tissue, is embedded in the connective tissue and muscle layer beneath the cornea. Light reaches the retina lining the concavity of the eye by passing through the pupil and then through the lens which fills the concavity of the eye (Figure *1*).

The retina, composed of sensory and supportive cells, is divided into 3 zones: nuclear, heavily pigmented, and photoreceptoral. The nuclear zone is lightly pigmented and contains the nuclei of the supportive and sensory cells. The supportive cells are narrow in this zone, containing little more than their darkly staining, irregularly shaped nuclei and a few melanosomes (Figure *2*). The sensory cells fill the broad spaces between the narrow supportive cells and in this region contain mitochondria, rough and smooth endoplasmic reticula, free ribosomes, single and clustered granules, and a large number of membrane-bounded vesicles about 800 Å in diameter, in addition to large, lightly staining, spherical nuclei (Figure *3*). The nuclei of supportive cells are more irregularly shaped and contain more heterochromatin.

In the pigmented zone, slender extensions of the sensory cells interdigitate in a complex manner with heavily pigmented columns of supportive cells. In this region the sup-

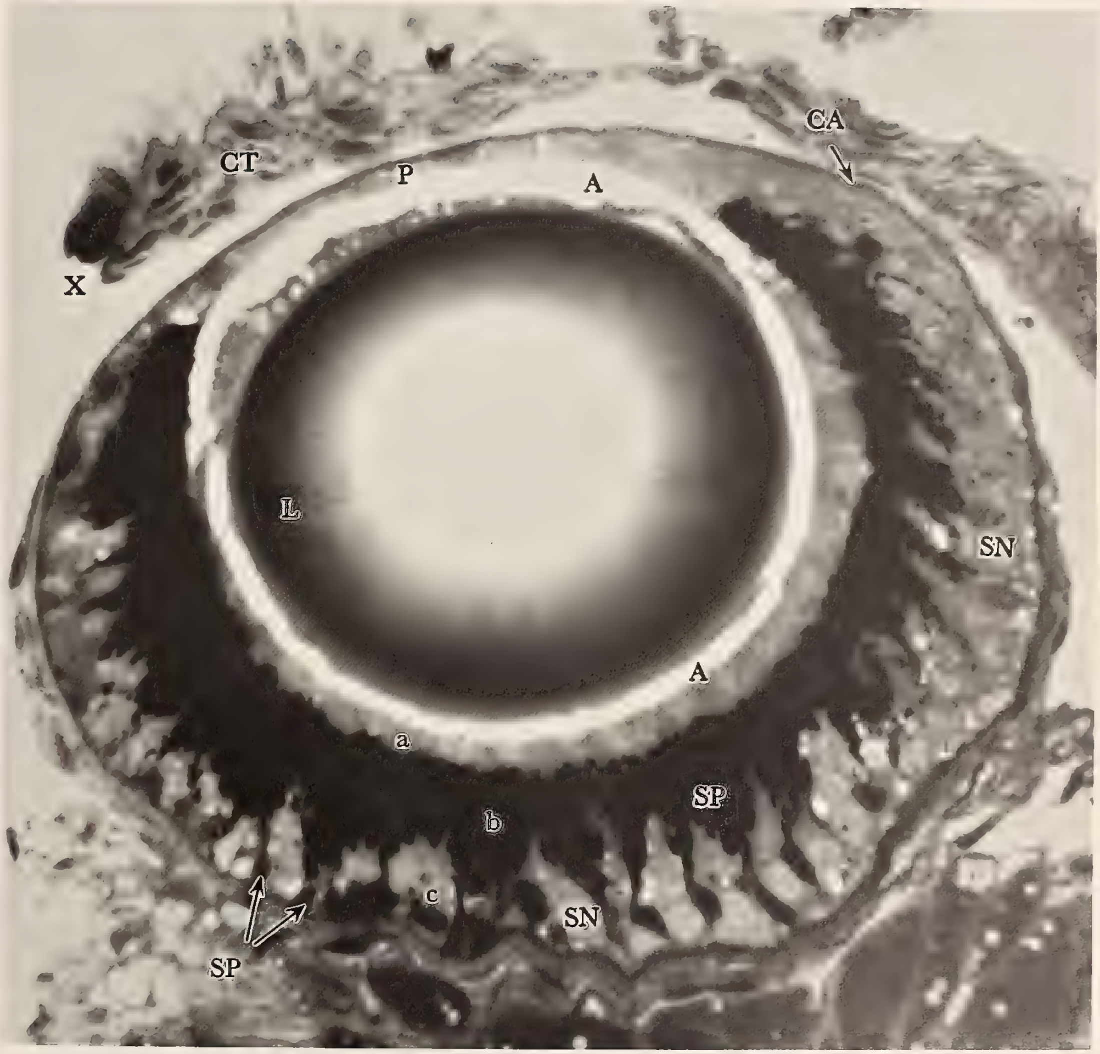

Figure *1*

Light micrograph of the eye showing: pupil (P), lens (L), the central region of which has not been preserved, shrinkage artifact (A), sensory cells (SN), supportive cells (SP), capsule (CA), connective tissue (CT), which has been cut at X, photoreceptoral zone (a), heavily pigmented zone (b), and nuclear zone (c). × 1000

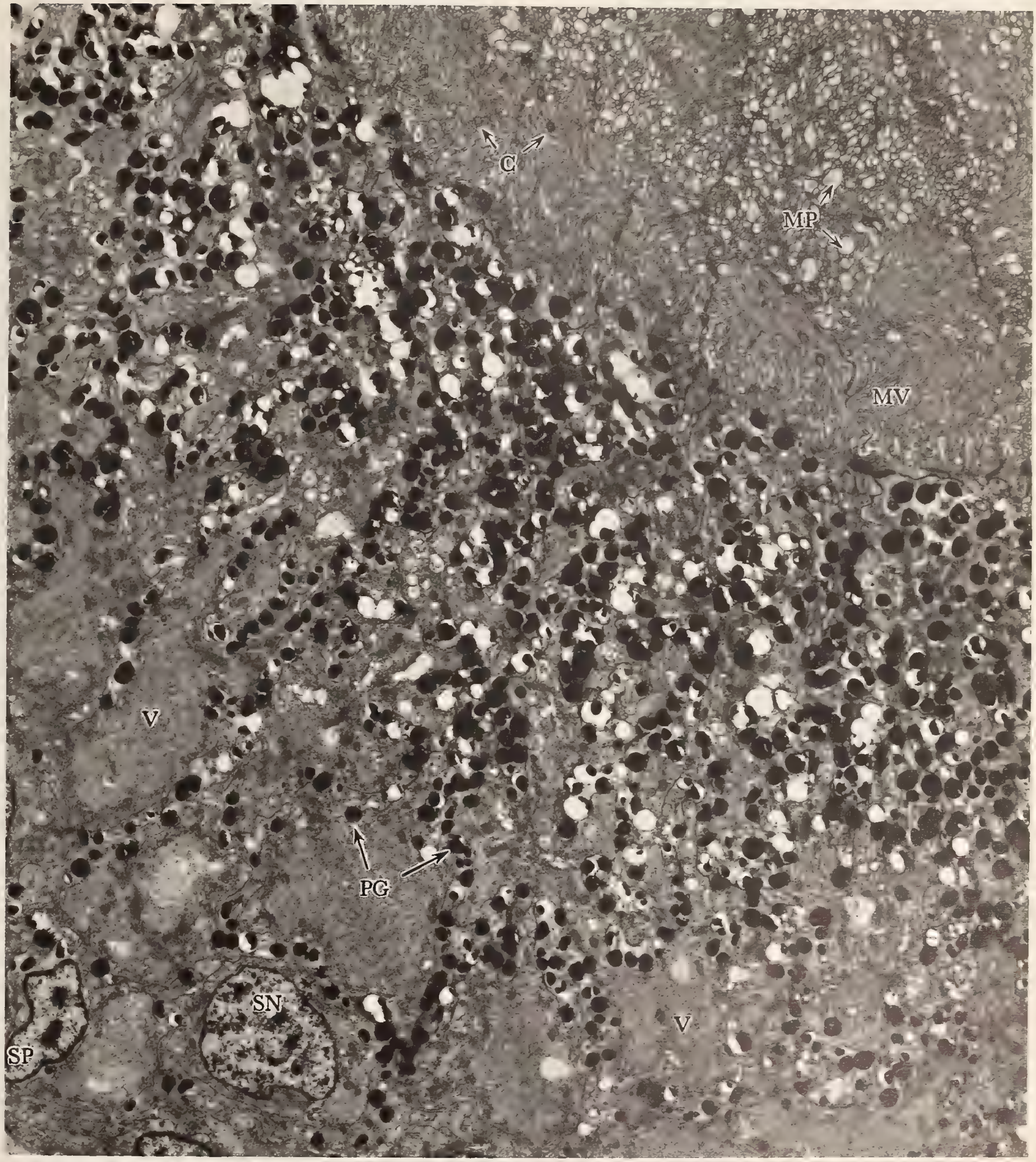

Figure 2

Section of the retina showing: supportive cells (SP), sensory cells (SN) containing 800 Å diameter vesicles (V), pigment granules (PG), microvilli (MV), cilia (C), membranous profiles (MP). × 5 100

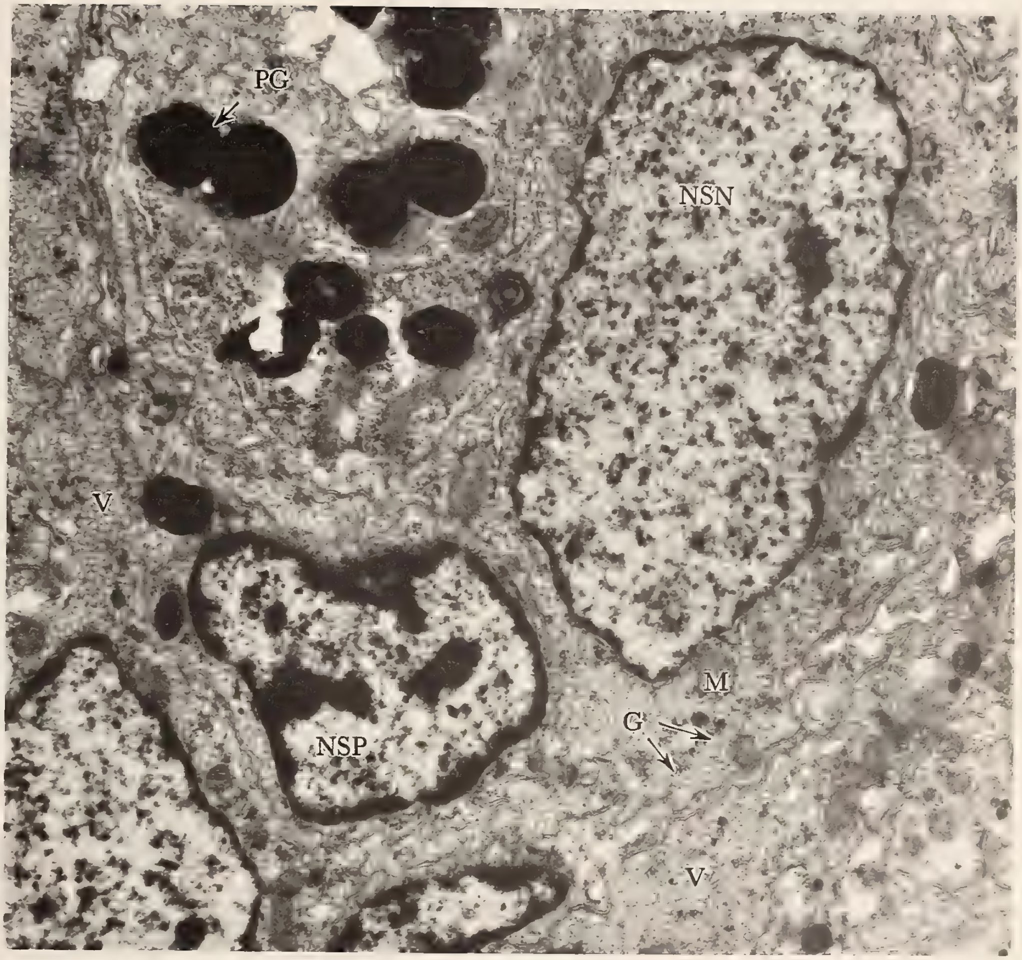

Figure 3

Nuclear zone showing: 800 Å diameter vesicles (V), granules (G), pigment granules (PG), mitochondria (M), nuclei of sensory cells (NSN) and supportive cells (NSP). × 18000

portive cells also contain rough endoplasmic reticulum and many glycogen granules. The sensory cells contain some melanin granules as well as many Golgi centers and 800 Å vesicles.

At the apical margin of the pigmented zone, each sensory cell broadens into an apical dome or hillock, containing mitochondria, glycogen granules, and many 800 Å vesicles. The cells are connected here by septate and adhering junctions (Figure *4*).

The photoreceptoral zone contains the rhabdomeres, irregular dense arrays of microvilli extending from the apical hillock of each sensory cell, and microvilli from the apices of the supportive cells. Among the microvilli of the rhabdomeres are numerous membranous profiles which are larger and more irregular than the microvilli. The cytoplasm within the profiles is less dense than in the microvilli. A finely granular material which is perhaps related to the dense granules that compose the lens is found in the microvilli of both types of cells, the membranous profiles and the extracellular space (Figure *5*). Cilia originating in small groups from the apical hillocks of the sensory cells are found among the microvilli (Figure *4*). These cilia have the typical 9 + 2 arrangement of microtubules.

The lens, which is extracellular, is composed of electron dense granular material. Adjacent to the lens is an irregular zone containing many relatively small diameter microvilli whose membranes are coated with dense fibrillar or granular material.

DISCUSSION

The eyes of *Littorina scutulata* and *L. littorea* are structurally very similar. Newell (1965) described a region between the lens and retina in *L. littorea,* a jelly-like structure known as the vitreous body. Charles (1966) confirmed the presence of the vitreous body in *L. littorea,* citing an unpublished electron microscopic study by Owen & Charles, and stated that the presence of a vitreous body was characteristic of littorinids. *Littorina scutulata,* however, like *Helix,* did not display such a structure, although some shrinkage artifact was seen in this area and there is obviously a humor which bathes the microvilli and lens.

The 800 Å diameter vesicles in *Littorina scutulata* do not occur in paracrystalline masses as found in *Helix* by Eakin & Brandenburger, but they look identical in every other way. The Golgi centers from which they appear to originate are located more apically in *L. scutulata* than in *Helix.* Charles (1966) did not mention such vesicles in *L. littorea,* but we have found them difficult to preserve in *L. scutulata.*

The clusters of granules which occur among the 800 Å vesicles are similar in *Littorina scutulata* and *Helix.* Eakin & Brandenburger (1967c) suggested that these granules are glycogen.

Irregular arrays of microvilli project from the sensory cells of *Littorina scutulata.* They extend to the lens but become less dense near it. Between the rhabdomeres and the lens, the granules in the extracellular humor seem to be forming the lens, contributing to the irregularity of the border between the lens and the rhabdomeres. According to Charles (1966) the microvilli of each photoreceptoral cell in *L. littorea* clump around the axial cilium forming a "terminal club" which projects into the vitreous material. In *L. scutulata* the cilia are not necessarily axial nor do the microvilli clump about them.

The rhabdomeres of the adult *Littorina scutulata* closely resemble the arrangement found in the 14-day embryo of *Helix* in which the microvilli are twisted and irregular. In adult *Helix* the microvilli are arranged in straight rows with only the central members of each apical hillock twisted (Eakin & Brandenburger, 1967b). The membranous profiles in the photoreceptoral region of *L. scutulata* probably represent microvilli of the rhabdomeres expanded by artifact during fixation.

The cilia among the microvilli of both *Helix* and *Littorina scutulata* are of the 9 + 2 type, whereas the axonemes of nearly all ciliary photoreceptors lack the central pair of microtubules as well as the arms of the A microtubule (Eakin, 1968). Although more abundant than in *Helix,* these cilia do not give rise to microvilli. As with *Helix,* they are probably present because the eye was formed from an infolding of ciliated ectoderm during embryonic development. These eyes are thus rhabdomeric. The close similarity between the structure of the eyes of *Helix* and *Littorina* shows that they are most likely homologous even though they have slightly different locations.

ACKNOWLEDGMENTS

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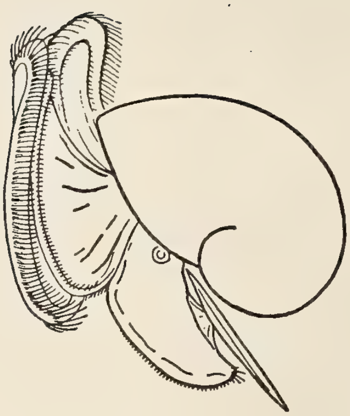

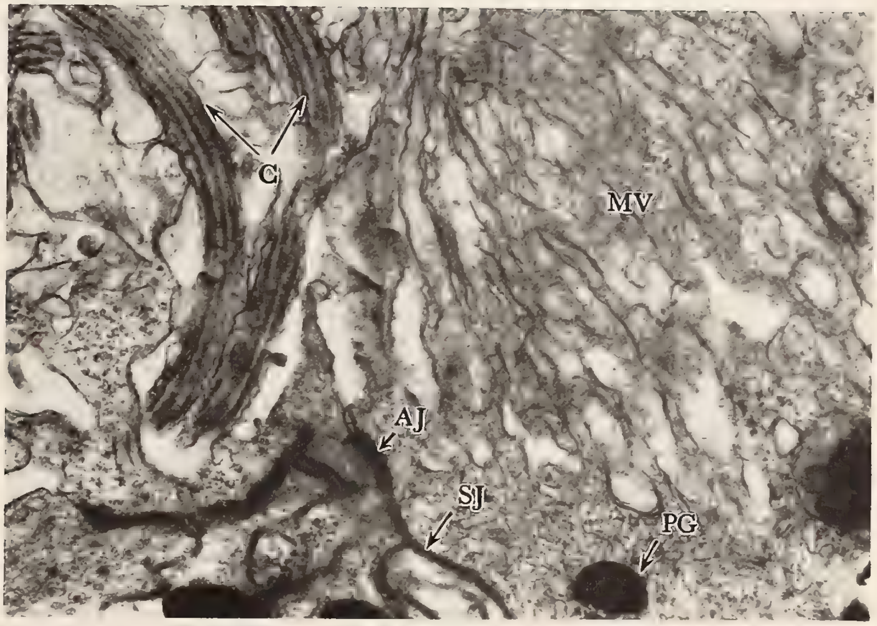

Figure 4

Apices of the sensory and supportive cells showing: adhering junctions (AJ), septate junctions (SJ), pigment granules (PG), microvilli (MV), cilia (C). × 18000

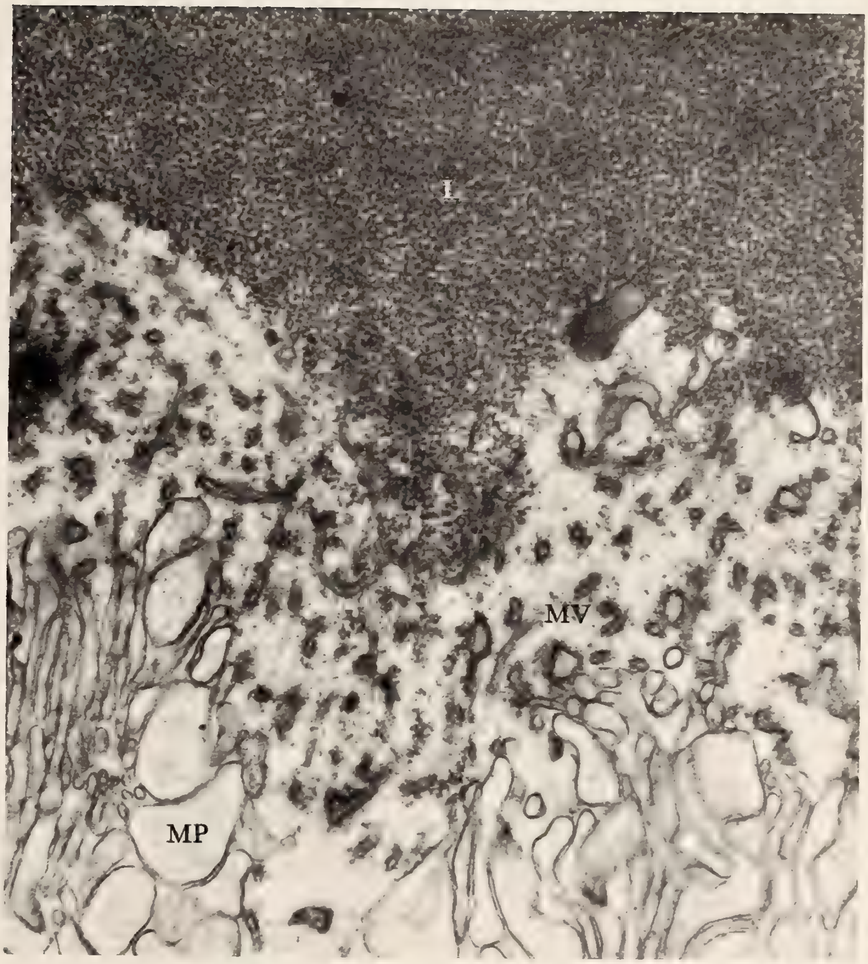

Figure 5

Irregular border between the lens and rhabdomeres showing: lens (L), microvilli (MV), membranous profiles (MP). × 14000

Physiology of the Pulmonate Reproductive Tract: [1] Location of Spermatozoa in Isolated, Self-Fertilizing Succinid Snails

(with a Discussion of Pulmonate Tract Terminology)

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(1 Plate; 1 Text figure)

INTRODUCTION

Cain in 1956 concluded her paper on fertilization in *Lymnaea* as follows: "The problems of the location of fertilization and the function of the seminal receptacle still remain unresolved." Despite the great strides in biology during the past 17 years, this statement is as true today as it was then, and it could be extended to cover several other aspects of the pulmonate reproductive tract. Familiarity with the elusive nature of these problems, and with the importance of snail breeding to medical malacology led me to carry out this study.

The physiological context of these problems is as follows. The simultaneous hermaphroditism typical of pulmonate snails is accompanied, in many species, both basommatophoran and stylommatophoran (see Patterson, 1970), by the ability to self-fertilize. The possibility of parthenogenesis has been widely investigated and has been ruled out in all species studied (Larambergue, 1939). Although there is controversy about the situation in particular species (Cain, 1956), it is probable that in normally breeding populations of snails, copulation followed by cross-fertilization is the mode of reproduction most commonly employed. The work of Ikeda & Mura (1934, *Bradybaena similaris stimpsoni* (Férussac)) crossing banded and unbanded snails, together with Cain's (1956, *Lymnaea stagnalis appressa* Say, 1817) work, extended recently by Richards (1970, 1973, *Biomphalaria glabrata* (Say, 1818)), in which albino and wild-type basommatophorans have been raised in isolation and then allowed to cross-copulate, has given us valuable data on dominance of allosperms and their longevity in the 'foreign' reproductive tract.

Some enigmatic problems are raised by these data. (1) By what means do allosperms dominate over autosperms in the fertilization of ova? (2) Where are the allosperms stored between copulation and fertilization? – an interval which may last up to 116 days in *Lymnaea stagnalis* (Linnaeus, 1758) (Cain, 1956), and more than a year in certain helicids (Larambergue, 1939).

In attempting to answer the second of these questions one is faced with histological data which further extend the problem. In normal adult pulmonates grown in mass culture (individuals not isolated), mature sperms are found possibly in 3 places – the seminal vesicles (ovotestis duct), the spermatheca, and the gonad, though it is doubtful whether sperms found in the latter are quite mature since it is thought that immediately upon maturation pulmonate sperms leave the gonad and enter the seminal vesicles where they are stored (Aubry, 1954). It has been consistently shown (see Larambergue, 1939; Bayne, 1970) that sperms are broken down in the spermatheca[3]. Therefore, apparently only the seminal vesicles remain as a possible storage site for allosperms between the time that they are received at copulation and the time they are used in fertilization. Within the seminal vesicles

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[3] Breakdown consists most noticeably of a loss of the sperm tail (Bayne, 1970). Ikeda (1937) considered this to be equivalent to a maturation after which the sperms could fertilize. Most reports, however, indicate that sperms are tailed at the time of fertilization (Larambergue, 1939b, Perrot, 1939).

numerous autosperms are stored; auto- and allosperms are microscopically indistinguishable, so that confirmation of this as an hypothetical storage site is not possible by routine microtechnique. The genera *Succinea* (RIGBY, 1965) and *Anguispira* (GUGLER, 1964) are exceptions in that they are reported to possess receptacula seminis, at the base of the ovotestis duct, in which oriented allosperms may be found.

In attempting to answer the first of the two questions above, two theories may be proposed: **a**) spermatozoa are not capable of fertilization until they have mingled with secretions from the pallial reproductive tract[4] – that is, they require capacitation or physiological maturation; or **b**) ova are not capable of being fertilized until they reach the site at which allosperms are situated at the time of fertilization – that is, the absence of fertilization during the passage of ova through the dense mass of sperms in the seminal vesicles is due to the nature of the ova, not the nature of the sperms (IKEDA, 1937; PERROT, 1937; HORSTMANN, 1955). A third theory, proposed by PEREZ (1889), that the sperms in the seminal vesicles are resorbed prior to each oviposition, is unacceptable in light of more recent reports of ova and sperms being seen together in the seminal vesicles of ovipositing pulmonates (PERROT, 1937; ABDEL-MALEK, 1954; DUNCAN, 1956; this study).

Before a full understanding of the functioning of the pulmonate reproductive tract is possible, a great research effort is necessary involving many experiments on many different species. On account of two reproductive features, *Succinea grosvenori* (Lea, 1864) was chosen for the first of these experiments. Firstly, succinid snails possess 2 diverticula, thought to be receptacula seminis, in the region of the ovotestis duct-albumen gland junction (Figure 1) (RIGBY, 1965). Secondly, *S. grosvenori* has been shown to reproduce in isolation (PATTERSON, 1970). The disputed relationships of the family Succineidae (BURCH & PATTERSON, 1968) added further interest.

If sperms must undergo some physiological maturation, possibly by encountering some secretion(s) in the pallial reproductive tract prior to self-fertilization, then a study of the location of sperms in the reproductive tracts of isolated, self-fertilizing succinids should give some valuable data when examined in snails at various stages of reproductive activity. The receptacula seminis might be considered as likely sites for such maturation, but it has also been suggested (IKEDA, 1929; SOOS, 1935) that maturation occurs in the spermatheca (=bursa copulatrix). One other feature of reproductive physiology might be further elucidated by such a study; that is the role of the 'prostate,' a gland whose function has not been adequately documented in any pulmonate (BAYNE, 1967).

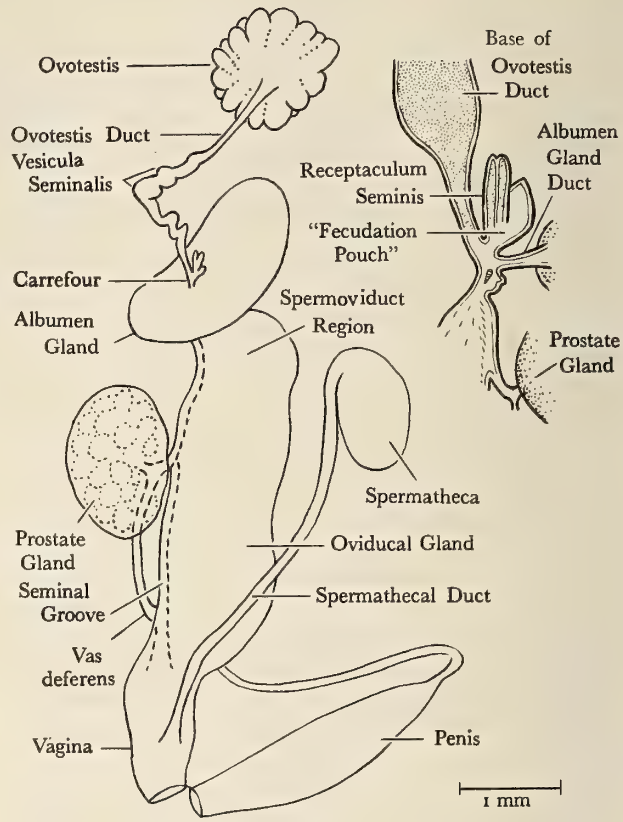

Figure 2

Reports by LAMS (1910, *Arion empiricorum* Férussac), CRABB (1927, *Lymnaea stagnalis appressa*), AUBRY (1955, *L. stagnalis*) and LANZA & QUATTRINI (1964, *Vaginulus borellianus* (Colosi) and *Laevicaulis alta* Férussac, 1812) that fertilization takes place within the gonads of self-fertilizing pulmonates are consistent with the recent report by BRISSON (1968) that in *Bulinus truncatus* Audouin intra-gonadal fertilization and development can be induced by removal of more anterior parts of the repro-

[4] It might seem that a more meaningful theory would postulate that this capability is acquired in the process of sperm exchange during copulation (GRATIOLET, 1851), but such a statement would leave no room for the self-fertilizing which can occur if there is no copulation, *e. g.*, in isolated individuals, and possibly in aphallic populations like *Bulinus truncatus*.

ductive tract. These reports would suggest that a physiological maturation of sperms and eggs does not require a mixing with secretions of the pallial reproductive tract. Instead a situation seems apparent in which a barrier to self-fertilization is eventually overcome by gametes if allosperms are not received over a long period. Certain species exhibit a lower fecundity if grown in isolation (IKEDA & MURA, 1934; LARAMBERGUE, 1939; LAVIOLETTE, 1954; BAYNE, 1970); many, hower, do not suffer this apparent disadvantage (CRABB, 1927; IKEDA, 1937; LANZA & QUATTRINI, 1964).

In this paper we are concerned with the mechanism whereby self-fertilization is normally avoided, but remains a possible alternative to cross-fertilization. We acknowledge that this flexible barrier to self-fertilization may be seated in the sperm or in the egg, or in both. The problems are very elusive of investigation. We are therefore asking, if the barrier is seated in the sperm:

i) must the fertilizing sperm (be they auto- or allosperms) be capacitated as in mammals?

ii) if so, what secretions are involved?

Data gathered during this research provide the first evidence that prostatic secretion may be important in the process of self-fertilization, in addition to its documented role in copulation, and its possible role in egg mass formation (BAYNE, 1967).

MATERIALS AND METHODS

Two species were used in the expectation that any existing intra-generic variation would be apparent: *Succinea grosvenori*, 9th generation in laboratory culture, and *S. unicolor* Tryon, 1866, 8th generation in laboratory culture. Six-day old specimens of *S. grosvenori* and 5-day old specimens of *S. unicolor* were placed individually into separate, large Petri dishes prepared for culture as described by PATTERSON (1970). The snails were fed lettuce, powdered chalk, Cerophyll[5] (a finely ground preparation of a mixture of cereal grasses) and water. Daily attention was necessary in order to maintain adequately clean and healthy conditions. At the ages shown in the Table specimens were killed by submersion in alcoholic Bouin's fixative. They were serially sectioned in paraffin wax at 7 μm and stained with azan-Mallory (PANTIN, 1964). The sections were all examined for the locations of sperms and for observations on the state of the various reproductive glands. Viable eggs were obtained from the specimens kept for the longest times.

[5] No longer commercially available.

Table 1

Events in the Development and Functioning of the Reproductive Tracts of Both Succinid Species

No.	Date fixed	Age (wks)	Shell length (mm)	Comments (s. v. = seminal vesicle; pros = prostate; alb. = albumen)
Succinea grosvenori				
2	6/VI 1969	4	4.2	Maturing ova and sperm; s. v. + sperm; primordial tract
3	6/VI	4	3.6	Sp-tids and oogonia, no s. v. or sperm; primordial tract
4	10/VI	4.5	3.8	Well developed gonad; s. v. + sperm; tract glandular
6	13/VI	5	3.7	Sp-gonia + sp-tids, no sperm, very primordial tract
7	13/VI	5	2.0	Sperm (few) in s. v.; primordial tract
10	17/VI	5.5	5.5	Sperm in s. v.; glands starting to accumulate secretion
11	23/VI	6.5	7.5	Sperm in s. v.; tract well developed
13	26/VI	7	5.0	Died just prior to fixation; sperm in s. v.; glands mature
14	28/VI	7.3	7.3	1 batch eggs laid; sperm in s. v.; alb and pros secreting; few sperm in enlarged fecundation pouch
15	30/VI	7.5	?	3 batches eggs laid (26/VI, 28/VI; 30/VI); sperm in s. v.; prostate secretion in seminal groove
Succinea unicolor				
1	6/VI	4	3.8	Possible gonia
5	10/VI	4.5	5.0	Sp-gonia and sp-tids, no sperm; primordial tract
8	13/VI	5	5.2	Oocytes and sperm; small s. v.; primordial tract
9	17/VI	5.5	5.5	Oocytes and sperm; small s. v.; primordial tract
12	23/VI	6.5	6.8	Sperm in s. v.; glands maturing
16	2/VII	7.7	8.2	Sperm in s. v.; some free alb. gd. secretion; pros poorly developed
17	11/VIII	13.5	8.0	9 eggs laid, ova in s. v.; no sperm in carrefour complex; alb. gd. + secretion in lumen; pros + secretion

RESULTS

Maturation of the Reproductive Tract

As with all pulmonate organ systems, the maturation of the reproductive system lacks clear-cut physiological stages. The development of a mature reproductive tract is a gradual process which begins early and is subject to considerable variations in rates between individuals.

Specimens of *Succinea grosvenori* matured a little earlier in this study than *S. unicolor*. Four weeks after hatching, stages of both male and female gametes were found in the young gonad of *S. grosvenori,* and in one specimen the ovotestis duct contained a small mass of sperms, thus representing the early seminal vesicle. At this age the pallial reproductive tract was merely a cord of undifferentiated cells. Whereas 2 specimens at 5 weeks still had primordial tracts, one specimen at 4½ weeks had a glandular tract, though not yet fully mature. One specimen at 5 weeks did not even contain any sperm; the other had a few in the seminal vesicle. The only specimen fixed at 5½ weeks contained sperms in the seminal vesicle, and the tract was becoming glandular, with accumulation of secretion beginning. All specimens aged 6½ weeks or more had histologically mature reproductive tracts.

Succinea unicolor at 4 weeks contained the earliest rudiments of a gonad containing only undifferentiated '-gonia.' No tract rudiment was recognized. By 4½ weeks such a rudiment was discernible, and spermatogenesis was occurring but no sperms were present in the ovotestis duct. At 5 and 5½ weeks both oocytes and sperms were present in the gonad and a few sperms were in the ovotestis duct; the tract was, however, still rudimentary and non-glandular. Maturation of the pallial glands was in progress at 6½ weeks. By 7.7 weeks the tract was mature. The late laying of this species (13½ weeks) may have been due to a requirement for more water than is necessary for normal growth, as oviposition occurred a few hours after an increase in the amount of free water in the container. (In the Basommatophora, a change of water often stimulates oviposition.)

Location of Spermatozoa

In all mature and maturing snails prior to egg laying, sperms were restricted to the gonads and seminal vesicles. In one specimen which had laid eggs, a few sperms were present in the 'fecundation pouch.' In snails raised in isolation sperms were absent, both prior to and after egg laying, from the receptacula seminis and from the spermatheca.

Two specimens of *Succinea grosvenori* which had been grown in communal containers were sectioned. Sperms were found in the receptacula seminis of both; poor fixation precludes a definite statement as to the contents of the spermatheca of one of these. The other contained filamentous material resembling sperm remains.

Other Observations

The conditions of the 'prostate' gland and the spermatheca of isolated specimens were significant. The spermatheca did not remain empty in the absence of copulation; in mature isolated individuals it always contained a large bolus of apparent detrital mucoid material which took a blue colour with Mallory III. The source of this material is unknown. The spermathecal duct is very narrow and not capable of much enlargement; it seems likely that the epithelium lining the spermatheca secretes some of the material in the bolus.

The most surprising finding was that in snails which had laid eggs the 'prostate' glands had always been actively secreting (Figure *1*a). Prostatic secretion was present in the lumina of the gland and was found to fill the ciliated 'seminal' groove of the lower oviduct of specimen 15 all the way to the vagina.

Four ova were present in the ovotestis of specimen 17. They were located within the mass of sperms in the seminal vesicle (Figure *1*b). It is noteworthy that these ova were not near the wall of the seminal vesicle where they might have been transported by epithelial cilia. A similar situation has been reported in *Physa fontinalis* (Linnaeus 1758) (Duncan 1958).

DISCUSSION

The results presented here are not entirely consistent with other published data on pulmonates. Ikeda (1937) reported that even in isolated *Philomycus bilineatus* (Rafinesque), a stylommatophoran, sperms were found in the spermatheca; but Colton's (1912, *Lymnaea columella* Say, 1817) and Larambergue's results (1939, *Bulinus contortus* Michaud, 1889 = *B. truncatus* Audouin), together with those of Azevedo, Costa Faro & Goncalves (1959, *Biomphalaria glabrata*) – all basommatophorans – like my own showed no sperms in the spermathecae of virgins. Also, fertilization did not occur within the gonad as has been described for certain other species (Lams, 1910; Crabb, 1927; Aubry, 1955; Lanza & Quattrini, 1964). These inconsistencies may be taken as indicative of a considerable interspecific variation in the physiology of the pulmonate reproductive tract.

Figure 1a

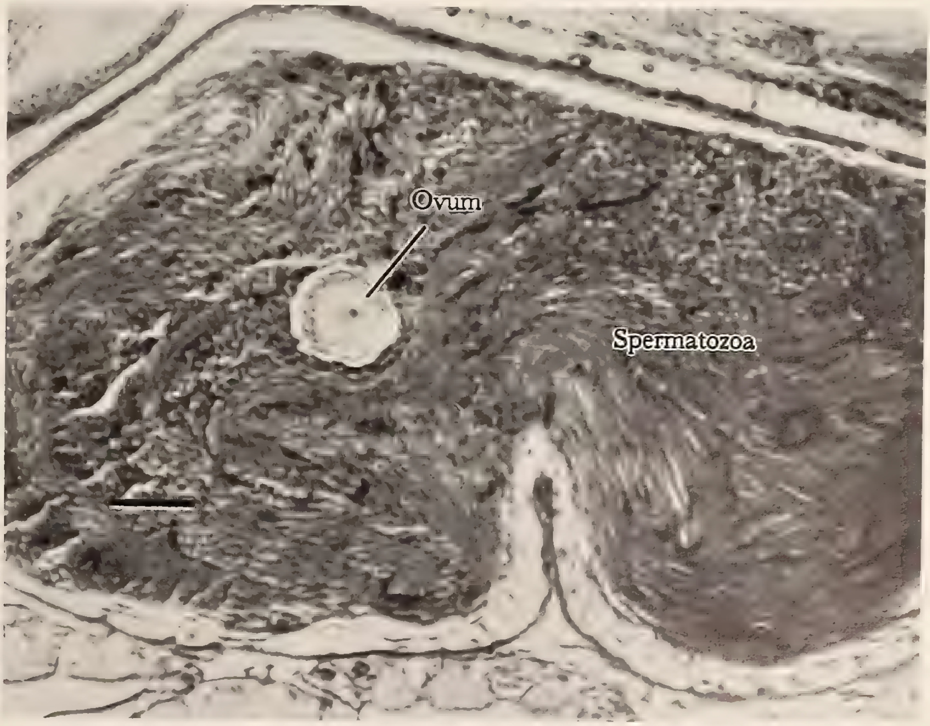

Figure 1b

Indications from this study indicate that if capacitation occurs, neither the receptacula seminis nor the spermatheca are involved. The active secretion of the 'prostate' reported here supports the idea that this organ may be functional not only in copulation but also in oviposition or fertilization or both (BAYNE, 1967). The presence of prostatic secretion in the ciliated channel of the oviduct indicates that it may be concerned with any capacitation which may occur.

Although the terms 'fertilization pocket' and 'fecundation pouch' are widely applied to a small chamber which opens into the carrefour complex, actual evidence of its function is scanty. RIGBY (1965) stated that it aggregates sperm packets and expels them into the male part of the spermoviduct. She also stated that it is the site of fertilization, though this was not based on actual observations. The presence here of sperms in one isolated individual which had laid eggs in the present study is further circumstantial evidence for its role as a fertilization pocket.

The absence of sperms from the receptacula seminis of isolated snails and their presence there in snails grown communally also amounts to strong but circumstantial evidence that these 2 blind-ending pockets are indeed the storage sites for allosperms. The equivalent site in basommatophorans is problematical (ALAPHILIPPE, 1959), there being no equivalent receptaculum seminis (RIGBY, 1965); it is expected that further research will elucidate this problem.

Reproductive Tract Terminology

A review of the literature on the morphology of the pulmonate reproductive tract clearly indicates that a confusion of terminology exists. This confusion can be particularly upsetting for investigators new to the area. In this short résumé suggestions are made, on the basis of (probable) function, as to the preferable names for all the major glands and ducts, excluding those of the terminal reproductive complex. It is hoped that this discussion will be beneficial to the field through its contribution to a standardized terminology.

The gonad, which produces both male and female gametes, is widely referred to as the hermaphrodite gland. While the organ is indeed hermaphrodite, this name does not specifically state that it produces gametes of both sexes, therefore the term **ovotestis** is preferred. The duct along which gametes pass from the ovotestis to the top (proximal end) of the pallial (glandular) reproductive tract is a hermaphrodite duct. However, since part of the pallial tract (spermoviduct) of the Stylommatophora is also hermaphrodite in function, the term **ovotestis duct** is preferable for this duct in the Stylommatophora. In all pulmonates part of this duct is modified as a seminal vesicle.

The word **'carrefour'** (French = crossroads, intersection) is acceptable as applicable to the junction of ducts at the base (distal end) of the ovotestis duct. It must be emphasized, however, that the term is not applicable to any specific structure, but rather to this general area, which is exceedingly complex and of great functional importance (HOLM, 1946; BRETSCHNEIDER, 1948; WU, 1972). The small size, delicate nature and complex relationships of the component ducts, pockets, and grooves make it difficult to unravel their true relationships. However, recently WALTER (1968, 1969) has published excellent accounts of the carrefours in *Lymnaea catascopium* (Say) and 3 species of *Bulinus*, and WU (1972) has made additional contributions for the genus *Bulinus*. However, in WALTER's words (1969) "The terminology expresses theoretical sequential stages in reproductive processes inferred solely from the structural relationships." In the absence of any functional studies his terminology must be accepted. Hopefully the validity of such terms as 'insemination chamber' and 'seminal reservoir' will be either proven or disproven as a result of future studies.

The terms **vesicula seminalis** (seminal vesicle), **receptaculum seminis** (seminal receptacle), **bursa copulatrix** and **spermatheca** are particularly subject to being confused. A **vesicula seminalis** is properly defined as an organ which stores autosperms. The term is therefore properly applied to that part of the pulmonate ovotestis duct which is more or less modified for sperm storage in the adult snail or slug. A **receptaculum seminis** is an organ which stores sperms received at copulation; it is therefore properly applied to the bilobed structure of that name in *Succinea* and in *Anguispira* (GUGLER, 1964). This term should not be used to refer to the spermatheca or bursa copulatrix discussed below. Most pulmonates evidently lack receptacula seminis as distinct organs. The term **bursa copulatrix** suggests a role in copulation and should not be used to designate the pocket which is usually attached to the vagina or atrium of pulmonates. Instead this pocket, or stalked pouch, should, at present, be referred to as the **spermatheca**. I say 'at present' because the role of this organ is as yet unclear. In pulmonates which produce a spermatophore (*i.e.*, certain stylommatophorans), the spermatheca probably dissolves this and releases the sperms, but this may not be its sole function. There are substantive data (Fretter, personal communication) which suggest that the spermatheca, which may

originally have functioned purely as a bursa copulatrix, has become less specific in its functions in several gastropod taxa. Thus, a terminology based solely on functional relationships cannot be entirely consistent between taxa when homologous structures have altered their functions in the course of evolution. Allosperms probably are passed to the spermatheca at copulation in all pulmonate species (WALTER, 1968), but those which are eventually active in fertilization probably do not remain long here. THOMPSON & BEBBINGTON (1969) have proposed that the equivalent organ in opisthobranchs be termed the 'gametolytic gland,' and indications are that this may be applicable for pulmonates also.

The gland which supplies the nutritive fluid in which the embryos develop is the album*e*n gland and the fluid it secretes is properly termed **albumen** (or perivitelline fluid of the egg mass), but not album*i*n, which refers to a specific group of proteins, whereas the nutritive fluid contains much more than protein (BAYNE, 1967).

The term **spermoviduct** has been somewhat confused, usage having been applied rarely to the ovotestis duct and more commonly to the common part of the pallial tract in stylommatophorans. In the Basommatophora – where the male and female ducts are separate from the carrefour – the term spermoviduct is not applicable. However, generally in the Stylommatophora the male and female glands share a common duct (though with possibly functionally separate canals or grooves) for much of the distance from the albumen gland to the vagina. Such a condition of male and female ducts should be called a spermoviduct (= ovispermiduct of some authors). The female glandular portion, which secretes the outer layers of the egg mass, is the oviducal gland. When the oviduct is separate, as in the Basommatophora, this glandular section (carrefour to vagina) has been called the **uterus**. The glandular cells are more or less different in distinct parts of this duct, and where the differences are marked, various names have been applied. Nidamental gland is an ancient term and should be dropped. The terms **muciparous gland** and **oothecal gland** reflect the functions of these organs and should be used, the former for the zone secreting the mucoid matrix of the egg mass, and the latter for the zone secreting the insoluble outer walls of the egg mass. These antero-posterior differences in the oviducal gland are more developed in the Basommatophora, a reflection of the different types of spawn in these and the Stylommatophora. In certain lymnaeids the uppermost region of the oviduct is more complex than this terminology suggests, and the terms used by WALTER (1968) in his beautifully thorough work should be followed. Below the oviducal gland the female duct passes into the **vagina**, a less glandular and more muscular tube. The **spermathecal duct** opens near to this region.

The male duct bears a different relation to the oviduct in the Basommatophora and the Stylommatophora. In the Stylommatophora the 2 lumina are confluent almost to the vagina, and in this case the 'prostate' secretes into the male groove of the spermoviduct. The Succineidae provide one exception to this: the male duct separates from the female duct at about the midpoint of the oviducal gland. It immediately receives the 'prostate' duct. From the point at which the male and female ducts become anatomically separate entities, the **vas deferens** leads to the penis. In the Basommatophora the male duct is distinct all the way from the carrefour to the penis; from its origin to the glandular – 'prostate' – region it is properly termed the **vas efferens**. The alternative 'sperm duct' is not adequately specific. In the Lymnaeidae the vas efferens is glandular and may be referred to as the upper 'prostate.' A 'prostate pouch' is present in certain lymnaeids (WALTER, 1968).

The glandular region of the male duct is known as the **'prostate'** gland. This term is not based upon knowledge of the gland's function, but rather on its anatomical position. The 'prostate' gland may secrete directly into the male channel (*e. g., Lymnaea*) or it may be separated off with its own duct (*e. g., Bulinus*). It is possible that the term as presently used refers to a complex of different glands; for a discussion of this see BAYNE, 1967. The duct which leads anteriorly from the 'prostate' to the penis is the **vas deferens**.

Within the oviducts of basommatophorans a channel runs from the lower regions up to the carrefour. This channel may be used to transport allosperms up to the site of fusion of gametes, and is thus called a **seminal groove**.

SUMMARY

In an attempt to clarify some of the problems of the physiology of the pulmonate reproductive tract, individual *Succinea grosvenori* and *S. unicolor* have been isolated soon after hatching and reared in individual containers. At various time intervals snails were fixed and sectioned. The distribution of sperms was examined at all ages up to and after egg-laying. Sperms were absent from the spermatheca and receptacula seminis of isolated snails, but were present in the vesicula seminalis. Surprisingly the 'prostate' gland had been actively secreting in all snails which had laid eggs. The implications are that the 'prostate' may be functional in some activity other than, though probably including, copulation. This activity might be sperm capacitation or egg mass production. The possibility that autosperms must undergo some maturation in the spermatheca prior to fertilization seems to be ruled out. No developing embryos were found in the gonads. It is

likely that the superior ability of allosperms to compete in pulmonate fertilization is due to a combination of ova 'ripeness' and allosperm location. Circumstantial evidence is reported that the receptacula seminis are indeed the storage sites for allosperms.

The terminology of the pulmonate reproductive tract is confused with respect to some terms. The nomenclature of certain parts is therefore discussed in light of their probable functions and the descriptive value of the names. A more consistent use of terms would be beneficial to the furtherance of knowledge.

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Hemochemistry and Hematology of the Aestivating Pond Snail *Pila globosa*

(Gastropoda : Ampullariidae)

BY

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(6 Tables)

INTRODUCTION

Dehydration, qualitative and quantitative changes in energy reserves, ions, intermediary metabolites and enzyme kinetics have been reported to occur in the tissues of *Pila globosa* (Say, 1822) during aestivation (Meenakshi, 1956; Raghupathiramireddy, 1967, and Vijaya Brahmanandam, 1972). Although the ionic composition of blood of *P. globosa* was reported by Saxena (1957), no report is available on the hemochemistry and hematology with reference to aestivation. It is essential to examine the hemochemistry and hematology of these snails during aestivation because the blood as transporting medium plays a pivotal role in the physiology of aestivation.

MATERIAL AND METHODS

1. Aestivation of Snails

Gastropod pond snails, *Pila globosa,* were collected from the suburbs of Bangalore and stocked in laboratory aquaria. While they were kept in aquaria, they were provided with cabbage slices and *Hydrilla,* a plant on which they normally feed. After they became used to laboratory conditions, a batch of them was made to aestivate by embedding them in dry mud in large wooden boxes, 60x35x 15 cm for the required period. Before burying, the snails were allowed to crawl in glass troughs overnight to dispel the mantle water. The temperature in the wooden box was maintained at 35° ± 2° C by heating with an electric lamp. Care was taken to maintain darkness by covering the bulb with tin foil. At one time about 50 to 100 snails were caused to aestivate; a new batch was started every month so that the aestivated snails were always at hand for analysis. In most cases the snails having aestivated for 6 months were selected for the investigations. Actively feeding snails from aquaria were used as controls.

2. Collection of Blood

The blood was collected from the snails by bleeding the animal at the visceral coils. Care was taken especially with the active snails to avoid mixing the mantle fluid with the blood. This was done by first draining off the mantle fluid and the animal was wiped well with filter paper before collecting the blood. The blood was used immediately for biochemical analysis.

3. Measurement of pH and osmotic pressure

The pH of the freshly collected blood was measured with a direct reading Phillips pH meter equipped with a glass and calomel electrode. The osmotic pressure of the blood was estimated by the melting point method as described by Giese (1968).

4. Protein estimations

The total proteins in measured samples of blood was estimated by biuret method (Layne, 1957), after precipitating the proteins with 10% trichloroacetic acid (TCA). Albumins and globulins of the blood were separated by ammonium sulphate fractionation (Cohn *et al.,* 1940) and estimated by biuret method. Bovine serum albumin (obtained ftom the Biochemical Unit, V. P. Chest Institute, New Delhi) was used as the standard for protein determinations. In some experiments, the precipitated protein after TCA treatment was dehydrated with alcohol, chloroform and ethanol (1:3) and dried with ether.

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The dried powder was weighed in a chemical balance to assess the protein content gravimetrically.

5. Non-protein fractions

The non-protein (NPN) and total a-acid contents of the TCA-treated blood filtrates were estimated by micro-kjeldhal method (Oser, 1965). The urea was estimated by nesslerization method (Oser, *op. cit.*) after hydrolysing the neutral deproteinized blood with urease.

6. Calcium-binding proteins

Per cent calcium-binding proteins were estimated in the following way according to Krishnamoorthy, 1963: 5% (wt/v) 0.25 M sucrose homogenates were prepared from the muscle of active and aestivated snails. The homogenates were centrifuged and the supernatants were dialysed overnight against 0.25 M sucrose solution. The dialysate was divided into 2 parts. In one part the protein content was estimated by the biuret method (Layne, 1957). To the other part an equal volume of 1 M $CaCl_2$ was added, thoroughly mixed and kept at 0° C for 30 minutes. The precipitate was centrifuged and suspended in distilled water, and 5% TCA was added. It was then centrifuged and the supernatant was discarded. The protein content was estimated by the biuret method. From the values obtained the percentage of proteins by calcium was calculated in each homogenate.

7. Carbohydrate composition of the blood

The deproteinized samples of the blood after TCA treatment were used to estimate the total sugars by the anthrone method (Hassid & Abraham, 1957). The blood glucose was estimated by glucostat (supplied by Worthington Biochemical Corporation) method. The blood pyruvate was estimated by the 2, 4 - dinitrophenyl hydrazine method (Oser, 1965) and the lactate by colorimetric-enzymatic method (Bruns & Bergmeyer, 1965).

8. Ionic composition of the blood

The chloride content of deproteinized blood was estimated titrimetrically (Milton & Waters, 1949). Blood calcium content was estimated by the method of Clark - Collip modifications of Kramer - Tisdall method (Oser, 1965). Magnesium was estimated by microtitration after its separation as the salt of 8-hydroxyquinoline (Milton & Waters, 1949). The blood sodium was determined by the method of Weinback (Oser, *op. cit.*). Potassium was determined by the method of Looney and Dyer (Oser, *op. cit.*).

9. Blood count

The blood cell count was pursued with the help of a hemocytometer using snail Ringer (Coles, 1969) as the dilution medium.

10. Assay of blood enzymes

The LDH activity of the blood was estimated spectrophotometrically (Neilands, 1957) by following the NA DH formation when the sample is incubated with sodium lactate and NAD. The glutamic-pyruvate transaminase (GPT) activity of the blood was estimated by the method of Reitman & Fraenkel (1957). The glycerol dehydrogenase activity of the blood was assayed spectrophotometrically according to Neilands (*op. cit.*), using glycerol and NAD in the assay medium. The glutamic dehydrogenase was assayed in the same way with glutamate and NAD in the assay medium.

RESULTS

As is evident from Table 1, aestivation in *Pila globosa* does not affect the pH of the blood, but the osmotic pressure was elevated 3 to 4 fold. Elevation in osmotic pressure may be due to an increase in soluble proteins, sugars, amino-acids or the salt composition of the blood, as these substances contribute to the osmotic relations of blood.

Table 1

Changes in the pH and Osmotic Pressure of Blood of Aestivating *Pila globosa*

	pH	Osmotic pressure atmospheres
Active snails	7.90±0.18 (12)	5.4 ±0.6 (6)
Aestivated snails	7.97±0.16 (12)	19.82±1.8 (6)
Incidence of change on aestivation	no change t=0.9660 p>0.1	Increase t=33.49 p<0.001

values are mean ± S. D.; number in parentheses is number of observations

Table 2 presents the data on the changes of nitrogenous compounds in the blood of *Pila globosa* during aestivation. Total blood proteins did not vary, whereas the total non-protein nitrogen, urea and total amino-acids, increased on

Table 2

Quantitative Changes in the Total Protein, Non-Protein Nitrogen Content and different Fractions of Proteins of *Pila globosa* during Aestivation

No.	Constituent	Active	Aestivated	Incidence of change on aestivation
1	Total protein gravimetric method (mg/ml) (6)	42 ± 1	39 ± 0.5	$t=6.003$ $p<0.001$ decrease
	Folin's method (mg/ml) (6)	40 ± 4.79	36 ± 3.05	$t=1.579$ $p>0.1$ no change
2	Total amino acid content glycine equivalents μg/ml) (6)	673 ±102	1246 ±249	$t=4.246$ $p<0.01$ increase
3	Total non-protein nitrogen (mg%) (6)	5.8± 0.66	9.6± 0.42	$t=10.72$ $p<0.001$ increase
4	Total albumin (mg/ml) (6)	21 ± 2.1	30 ± 1.9	$t=7.109$ $p<0.001$ increase
5	Total globulins (mg/ml) (6)	19 ± 1.5	7.8± 1.1	$t=15.92$ $p<0.001$ decrease
6	Urea (μg/ml) (6)	168 ± 33	216 ± 24	$t=2.595$ $p<0.01$ increase
7	Dry matter (μg/ml) (6)	42 ± 3.7	41 ± 1.8	$t=0.8983$ $p>0.1$ no change

values are mean ± S. D.; number in parentheses is number of observations

Table 3

Changes in the Ionic Composition of the Blood of *Pila globosa* during Aestivation

Ion	Active	Aestivated	Incidence of change on aestivation
Calcium (mg/100 ml)	22 ± 5.29 (7)	56± 12.9 (8)	$t=6.023$ $p<0.001$ increase
Magnesium (mg/100 ml)	15 ± 2.75 (7)	28± 10.08 (7)	$t=3.114$ $p<0.01$ increase
Sodium (mg/100 ml)	1890 ±175 (6)	3038± 233 (6)	$t=8.825$ $p<0.001$ increase
Potassium (mg/100 ml)	48 ± 10.4 (6)	62± 13.9 (6)	$t=1.806$ $p>0.1$ no change
Chloride (mgCl/100 ml)	119.5± 4.8 (6)	121± 7.9 (6)	$t=0.3626$ $p>0.1$ no change

values are mean ± S. D.; number in parentheses is number of observations

Table 4

Per cent Calcium-binding Proteins of Blood and Sucrose Soluble Fractions of Tissues of *Pila globosa* during Aestivation

Protein	Active snail	Aestivated snail	Incidence of change on aestivation
Blood proteins	5.23±0.93 (6)	5.98± 0.67 (6)	no change
Foot muscle proteins	17.58±6.84 (8)	44.18±11.71 (8)	increase
Mantle muscle proteins	19.32±5.68 (5)	48.38± 5.69 (5)	increase

values are mean ± S. D.; number in parentheses is number of observations

aestivation. Total albumins of the blood increased in contrast to total globulins. The dry matter did not change per unit volume of blood during aestivation.

Table 3 presents the changes in ionic composition of blood due to aestivation. Calcium, magnesium. and sodium concentrations increased, whereas chloride and potassium did not show any change on aestivation. The calcium-binding proteins of the foot and mantle increased but the blood Ca^{++}-binding proteins did not vary in concentration (Table 4).

Table 5 presents the quantitative changes in the carbohydrate composition of the blood due to aestivation. Total

Table 5

Quantitative Changes in the Carbohydrate Composition of Blood of *Pila globosa* during Aestivation

Constituent	mg/ml or μM/ml		Incidence of change on aestivation
	Active	Aestivated	
1 Total sugars	1.97 ± 0.21 (8)	1.57 ± 0.26 (8)	t=3.432 p<0.01 decrease
2 Glucose	1.58 ± 0.39 (7)	1.16 ± 0.026 (6)	t=2.437 p<0.01 decrease
3 l (+) lactate (μM/ml)	57 ± 19.6 (4)	44 ± 18.56 (4)	t=0.834 p>0.1 no change
4 Pyruvate (μg/ml)	20 ± 6.6 (8)	7.5 ± 1.4 (7)	t=4.576 p<0.01 decrease

values are mean ± S. D.; number in parentheses is number of observations

sugars, glucose and pyruvate decreased on aestivation, whereas the lactate did not vary much, contrary to MEENAKSHI's (1956) findings.

Table 6

Specific Activities of Certain Enzymes in the Blood of *Pila globosa* during Aestivation

Specific Activity	Active	Aestivated
1 LDH (units)	980 ± 21 (6)	568 ± 32 (6)
2 GPT (μg pyruvate/mg protein/hr)	12 ± 2.6 (6)	5.6 ± 1.4 (6)
3 Glycerol dehydrogenase (units)	244 ± 42 (6)	686 ± 48 (6)
4 Glutamic dehydrogenase (units)	128 ± 34 (6)	462 ± 18 (6)

values are mean ± S. D.; number in parentheses is number of observations

Table 6 illustrates that the specific activities of blood LDH and GPT decreased on aestivation in contrast to glycerol dehydrogenase and glutamic dehydrogenase.

Hematologically, blood shows variations in composition and also in differential count. Two types of cells, large and small, were identified. The large cell count was more or less the same (*i. e.,* 2.1 ± 0.09 thousands per ml) in aestivated snails, but the small cell count decreased and was 23.6 ± 2.16 thousands per ml in aestivated snails.

DISCUSSION

Dehydration has been noted by RAGHUPATHIRAMIREDDY (1967) and VIJAYA BRAHMANANDAM (1972) in the liver, mantle, and foot muscle of *Pila globosa* during aestivation. The present results indicate that there is no dehydration in the blood since the total proteins and total dry matter did not vary on aestivation (Table 2). Albumins, being water soluble proteins, are known to imbibe more water than the globulins (MAHLER & CORDES, 1966).

Increase in albumins (Table 2) on aestivation may help to prevent desiccation by way of water retention through imbibition.

During aestivation accumulation of nitrogenous wastes in the tissues occur (RHAGUPATHIRAMIREDDY & SWAMI, 1963). Concomitantly, accumulation of NPN reserves and urea content were observed in the present results (Table 2). The accumulation of these substances may be due to the lack of a medium for excretion. Increase in total blood amino acids on aestivation (Table 2) may suggest either higher degradation of tissue proteins or blood globulins (Table 2) and disintegration of smaller red cells.

Increase in ionic composition, like Ca^{++}, Mg^{++}, and Na^{++} on aestivation (Table 3) has its significance in contributing to the elevation of blood osmotic pressure (Table 1) and also in obviating the osmotic effects at tissue level which may prevail due to dehydration. Increase in Mg^{++} in body fluids of aestivating snails (MEENAKSHI, 1956; RAGHUPATHIRAMIREDDY, 1967) is known. These authors suggested that the dormancy of the snail may be due to the

anaesthetic property of the Mg^{++}. Increase in Ca^{++} may have significance in maintenance of calcium-binding proteins in tissues which are increased in concentration during aestivation (Table 4). It is probable that Ca^{++} may be secreted from the shell or mantle into the circulating fluids during dormancy which may cause this increase. Increase in ions did not affect the pH of the blood (Table 1).

The results on carbohydrate composition of the blood of aestivating animals indicate the metabolic patterns they experience. Decrease in total sugars, glucose and pyruvate levels (Table 5) may be due to the effect of starvation during aestivation. Decreased LDH activity (Table 6) reduced the oxidation of lactate and the pyruvate undergoes transaminations (Table 6) and hence the pyruvate level is decreased during aestivation. There is evidence (Krishnamoorthy & Vijaya Brahmanandam, 1970) that the reserve fats of tissues offer a source of energy.

SUMMARY

1. Hemochemistry and hematology of the aestivating pond snail *Pila globosa* with reference to aestivation was studied.
2. The pH of the blood was not affected as a consequence of aestivation, but the osmotic pressure was elevated 3 to 4-fold.
3. There was no dehydration in the blood as the total proteins and total dry matter did not vary on aestivation.
4. The carbohydrate composition of the blood of aestivating snails indicated the metabolic patterns they experience.
5. Ca^{++}, Mg^{++} and Na^{+} concentrations increased, whereas chloride and potassium did not show any change on aestivation.

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Morphological and Behavioral Adaptations to Desiccation in the Intertidal Limpet *Acmaea (Collisella) strigatella*

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(7 Text figures)

INTRODUCTION

THE DISTRIBUTION OF INTERTIDAL organisms on rocky shores is determined by a number of factors, among which tolerance of desiccation is generally recognized to be of importance. The absolute tolerance to desiccation probably determines the upper limits of the vertical range for most intertidal species (CONNELL, 1970). Studies of adaptations to desiccation in the gastropod mollusks have involved two distinct approaches. The first approach has been experimental, where the investigators have compared the abilities of individuals from different areas of the vertical range to withstand desiccating conditions (BROEKHUYSEN, 1940; BROWN, 1960; DAVIES, 1969; WALLACE, 1972). The second approach has involved the analysis of shell shape and size in limpet gastropods that occur at different levels in the intertidal zone (RUSSELL, 1907; ORTON, 1933; MOORE, 1934; RAO & GANAPATI, 1971). In these studies limpets occurring at higher levels were observed to be structurally different from limpets at lower levels. The forms from higher levels displayed a tall, conical shell, while those from lower levels had a flattened, conical profile with an enlarged shell circumference. The significance of these differences in shell morphology appears to be related to the increased water-holding capacity that the limpets at higher levels possess. The only study to clearly show this relationship was conducted by SEGAL (1956a) on the limpet *Acmaea (Collisella) limatula* Carpenter, 1864, at Palos Verdes, California. For a given body weight the shells of limpets from higher levels were thicker and had a smaller total internal volume than did those from lower levels. However, the smaller shell volume reported for specimens from higher levels was more than compensated for by the smaller size of the soft parts of the animals. This resulted in a greater extra-visceral volume (and therefore a greater water-holding capacity) in the *A. limatula* from higher levels. The present study extends the comparative approach of SEGAL (1956a) by examining extra-visceral space in *A. (C.) strigatella* Carpenter, 1864 [1] collected from the upper and lower portions of its vertical range on a concrete seawall.

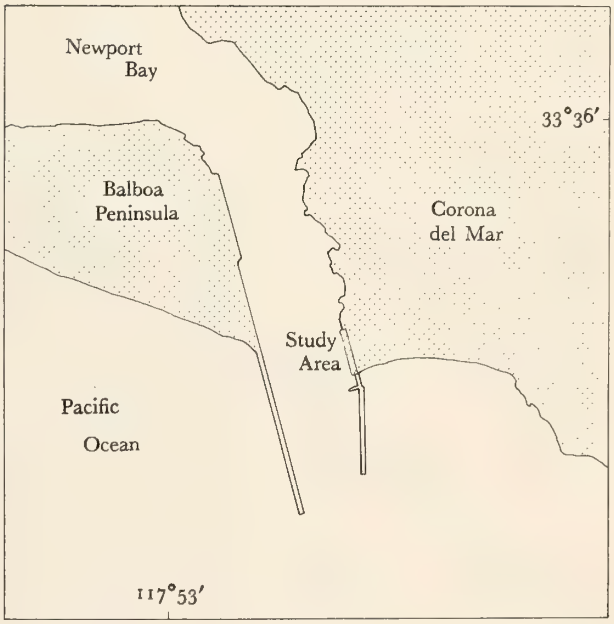

Figure 1

Location of Study Area in the Entrance Channel to Newport Bay, California, 33°35′36″ N Lat.; 117°52′38″ W Long.

[1] The taxonomic status of *Acmaea (Collisella) strigatella* was clarified recently by McLEAN (1969) who considered *A. paradigitalis* Fritchman, 1960 to be a synonym.

Behavioral responses to changes in desiccation stress by the limpet *Acmaea (Collisella) digitalis* Rathke, 1833 have been reported by FRANK (1965) and BREEN (1972). Both authors reported vertical migration by *A. digitalis* to higher levels in the intertidal zone during winter months. In the present study patterns of seasonal migration in *A. strigatella* are examined in relation to changes in desiccating influences.

METHODS

The study area (Figure 1) is located on the west-facing concrete seawall in the entrance channel to Newport Bay, Orange County, California. Specimens of *Acmaea strigatella* to be used for laboratory analysis were collected from a low-level sampling zone located between the tidal levels of +0.2 to +0.6m (= +0.5 to +2ft.) and from a

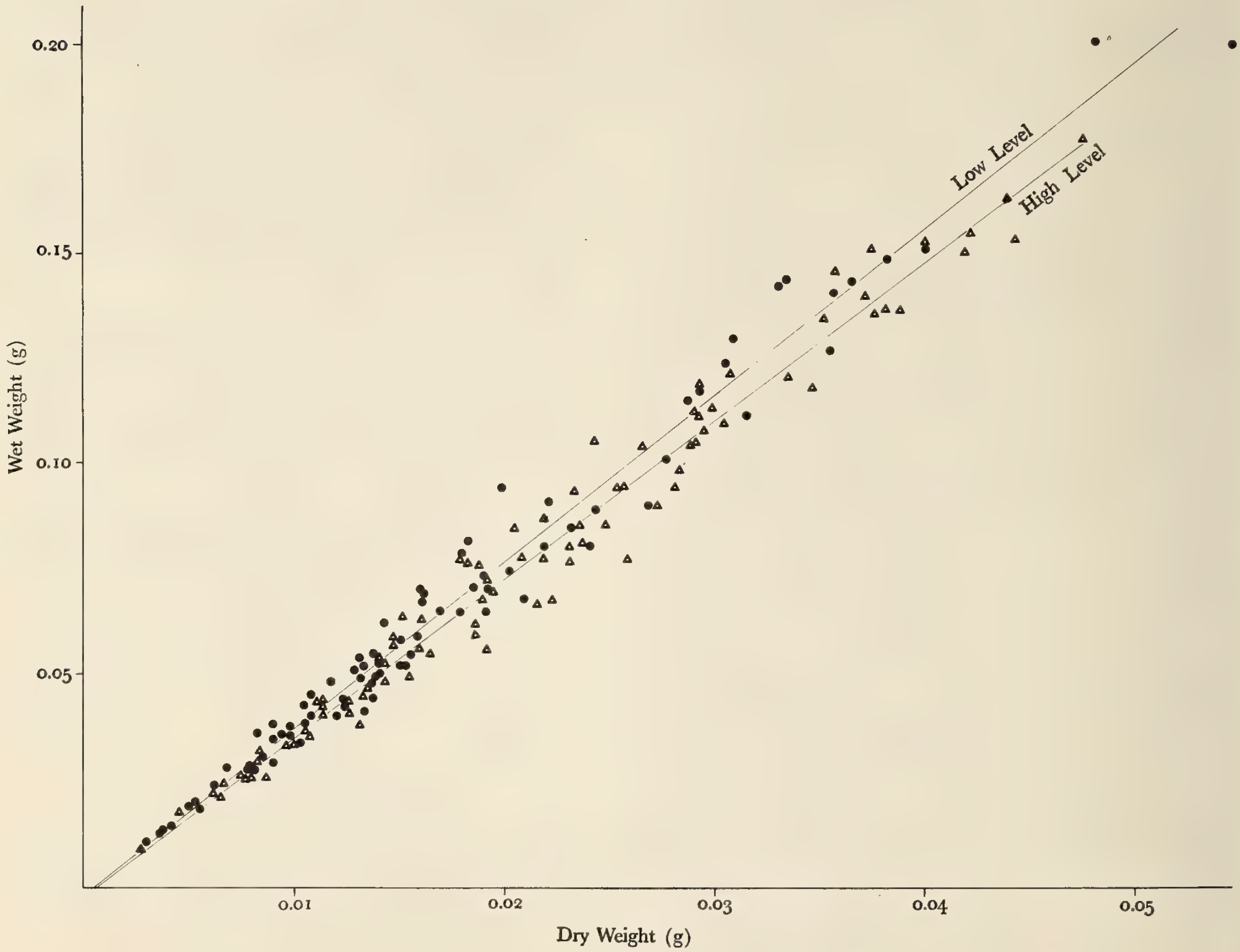

Figure 2

Relation between Fresh Wet Weight and Dry Weight in Specimens Collected in January and July 1971 from the High-Level (●, $Y = -0.003 + 3.771\ X$) and Low-Level (▲, $Y = -0.003 + 4.005\ X$) Sampling Zones

high-level sampling zone situated between +1.5 to +2.0 m (=+4.5 to +6ft.), relative to 0 Datum at Mean Lower Low Water. Collections were made during November and December 1970 and January, February and July 1971. Positive identification of questionable specimens of *A. strigatella* was resolved by analysis of the radular ribbons, following the method of FRITCHMAN (1960).

Extra-visceral volume was obtained as the difference between shell volume and soft part volume by an approach similar to that of SEGAL (1956a), with modifications that permitted the accurate measurement of very small (0.02 to 0.40 cm^3) specimens. Each shell was mounted on a lump of soft wax with the shell apex pointing downward and the lowest point on the shell rim in the line of sight of a horizontally-oriented dissecting microscope. The shell was then filled with n-butanol from a micrometer syringe that was read to the nearest 0.001 ml. Normal butanol was used because of its low surface tension and vapor pressure. A statistical test to estimate required sample size (DIXON & MASSEY, 1969: 80) indicated that 7 or more measurements were sometimes necessary to estimate volume for the larger shells, while as few as 4 trials were often adequate for smaller shells.

The body volumes of the limpets were obtained indirectly by dividing wet weight by a density value of 1.038g per cm^3. The density value was experimentally determined from 13 volume displacement trials each performed with 8 limpets of known total weight (95% confidence limits = 1.038 ± 0.021 g/cm^3). Freshly collected limpets were weighed to the nearest 0.001g. Although a consistent blotting procedure was employed prior to making each wet-weight measurement, small variations in blotting efficiency apparently were responsible for large differences in resultant wet-weight values. To surmount this problem, 186 limpets were collected from the high- and low-level sampling zones during January and July 1971. These specimens were blotted and weighed, and were then oven dried at 85°C to constant weight (usually 48 hours) and reweighed. These data displayed linear regressions for individuals from high-level and low-level sampling zones (Figure 2). An F test for comparison of slopes indicated that the 2 regressions were significantly different ($P < 0.05$). The wet weight values for all limpets used in the calculation of body volumes were determined from dry weight measurements, using the regression equations calculated in Figure 2.

The vertical movements of *Acmaea strigatella* were followed during the months of May to August 1971. On April 30, 22 individuals located between +1.0 and +1.5 m were marked with enamel paint, and their positions were recorded with respect to small reference spots of paint on the substrate. The marked limpets were allowed 24 hours to seek preferred positions on the substrate. The position of each individual on 1 May 1971 was then taken as the starting point from which vertical displacement was recorded during the daylight hours at about 10-day intervals.

RESULTS

Extra-Visceral Space

Data obtained from samples collected in November and December 1970, in January and February 1971 and in July 1971 were used to construct graphs (Figures 3, 4,

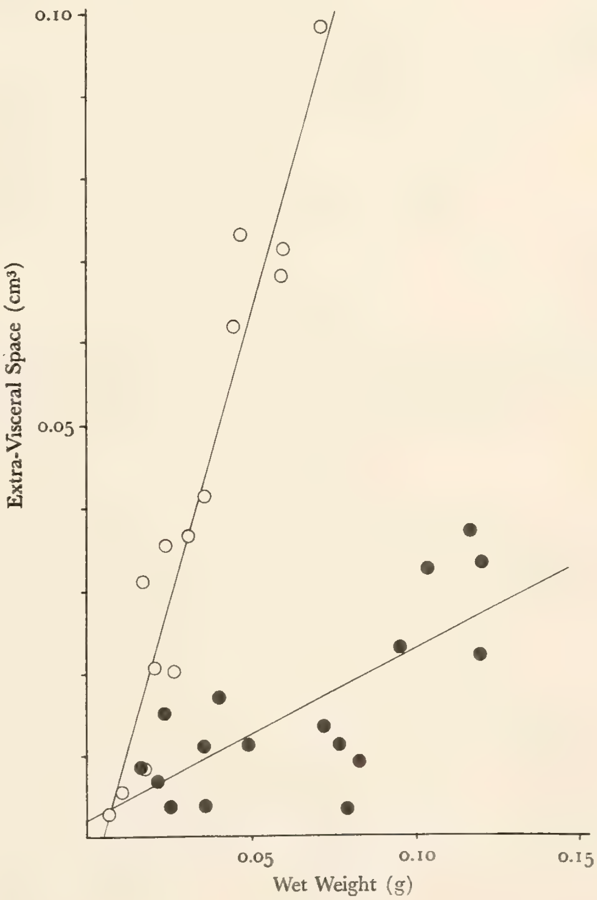

Figure 3

Relation between Wet Weight of Soft Parts and Size of the Extra-Visceral Space for Specimens from the High-Level (○, Y = −0.008 + 0.693X) and Low-Level (●, Y = 0.002 + 0.104X). Sampling Zones collected in November and December 1970.

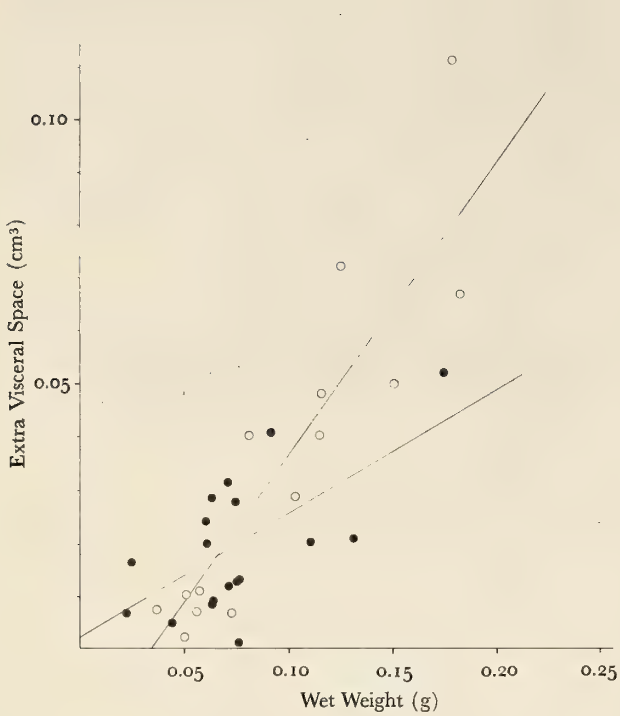

Figure 4

Relation between Wet Weight of Soft Parts and Size of the Extra-Visceral Space for Specimens from the High-Level (○, Y = −0.019 + 0.560X) and Low-Level (●, Y = 0.004 + 0.235X) Sampling Zones collected in January and February 1971.

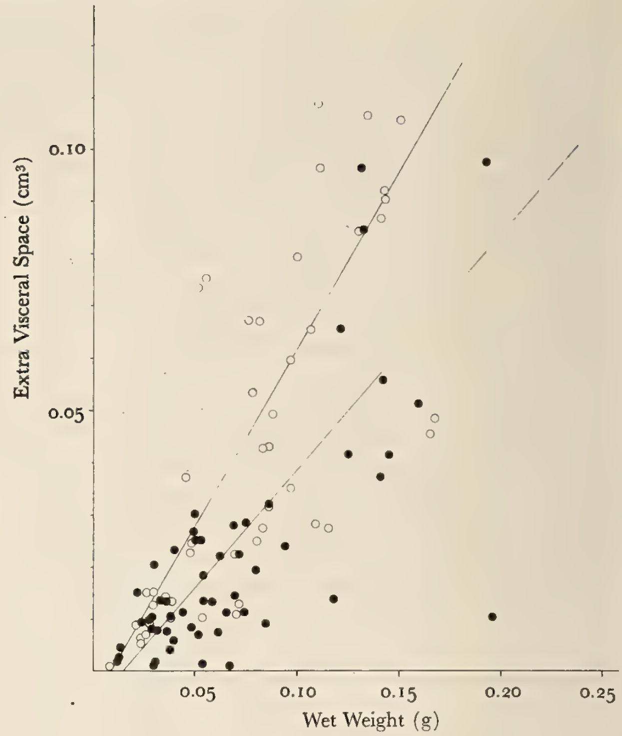

Figure 5

Relation between Wet Weight of Soft Parts and Size of the Extra-Visceral Space for Specimens from the High-Level (○, Y = −0.006 + 0.689X) and Low-Level (●, Y = −0.006 + 0.457X) Sampling Zones collected in July 1971.

and 5) relating the size of the extra-visceral space to the wet weight of limpets from the high- and low-level sampling zones. For each sampling period, the data from high- and low-level sampling zones were compared by analysis of covariance (DIXON & MASSEY, 1969). For November and December (Figure 3), F tests for comparison of variances and slopes revealed that high- and low-level samples differed significantly ($P < 0.001$). With the exception of small individuals, limpets of any given size (as measured by soft part weight) from the high-level sampling zone had larger extra-visceral spaces than did those from the low-level sampling zone. The regression lines in Figure 3 allow limpets of a given weight from each sample to be compared. For example, a high-level limpet weighing 0.030 g possesses an extra-visceral space of 0.037 cm^3 (corresponding to about 120% of its body volume), while the extra-visceral space of an 0.030 g low-level limpet is only 0.008 cm^3 (corresponding to only 27% of its body volume).

For the January-February 1971 sample (Figure 4) F tests indicated that the variances about the regression lines were not significantly different ($P > 0.05$), although the slopes were significantly different ($P < 0.005$). For the July 1971 sample (Figure 5), F tests indicated significantly different variances ($P < 0.05$) and slopes ($P < 0.005$). It is noteworthy that the slopes for the high-level samples in Figures 3 to 5 were reasonably consistent, while the slopes for the low-level samples were quite variable. These

latter slope differences suggest the hypothesis of vertical migrational movements by limpets on a seasonal basis, with the strongest vertical separation of high- from low-level forms occurring at the time of the November-December sampling.

Migration

Qualitative observations were made on the vertical distribution of *Acmaea strigatella* at the study area during November 1970 to February 1971. Fewer limpets were observed in the high-level sampling zone (+1.5 to +2.0 m) during January and February than during the preceding 2 months. Limpets in the high-level zone were rarely observed above +1.6m during January-February. These observations suggest that high mortality or a downward migration, or both, had occurred during December and January. Mortality cannot be ruled out as a causal explanation for the reduction in numbers in the high-level sampling zone. However, a downward migration is also

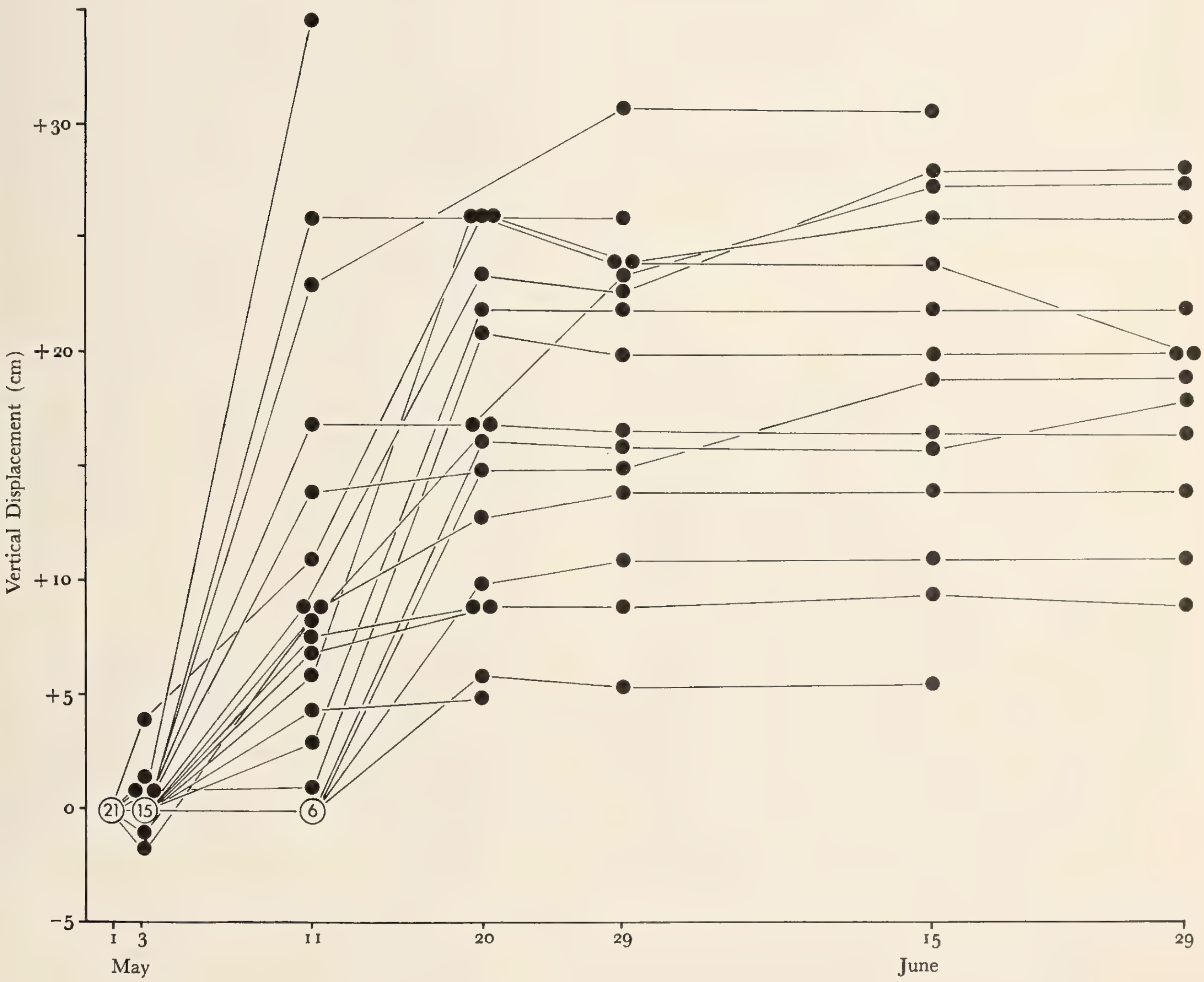

Figure 6

Vertical Movement of Marked Individuals as a Function of Time, Measured as Vertical Distance of Movement from Individual Starting Positions Established on 1 May 1971. The Vertical Movements of each Marked Limpet from one Date to the Next are indicated by Connecting Lines.

plausible, and could represent a behavioral response to increasing desiccation stress. A possible explanation of how desiccation stress could increase at this time of year will be presented in the discussion section.

During late April 1971 an observation was made that suggested the initiation of movement of limpets to higher levels. Several limpets were located at about +1.3 m bearing thalli of *Enteromorpha* sp. on their shells. At this time *Enteromorpha* sp. occurred only below +0.6 m. In order to follow the suspected upward migration of limpets after April, the movements of 22 marked individuals occurring between +1.0 and +1.5 m were recorded (Figure 6). The majority of individuals exhibited no net vertical displacement through May 3. By May 20, however, it was apparent that a dramatic upward migration had occurred. The mean upward displacement between May 1 and May 20 was 17.2 cm. The positions of marked limpets from May 20 to June 29 were remarkably stable. When the study area was visited in mid-July, insufficient numbers of marked individuals could be located, and monitoring was discontinued.

DISCUSSION

The comparative measurements of extra-visceral space for *Acmaea strigatella* from high- and low-level sampling zones during November and December 1970 (Figure 3) are in agreement with the results of Segal's (1956a) study on *A. limatula*. Both species possess a broad vertical range in the intertidal zone and distinct morphological differences within this vertical range were recorded. Reproductive and physiological differences within a limpet's vertical range would also be predicted, and have been reported for *A. limatula* by Segal (1956b) and Segal & Dehnel (1962), and for *A. (Collisella) scabra* (Gould, 1846) by Sutherland (1970). In the present study the comparison of wet to dry weight of limpet soft parts (Figure 2) suggests vertical differences in the osmotic state of the body fluid. *Acmaea strigatella* occurring at higher levels had wet weights that averaged 6% less than wet weights of individuals at lower levels having the same dry weight.

Seasonal differences in samples collected from the low-level sampling zone were suggested by the data of Figures 3, 4, and 5, and may be interpreted in relation to hypothetical vertical migratory movements. The slope for the low-level regression line was steeper for the January-February sample ($b = 0.235$) than for the November-December sample ($b = 0.104$). This change in slope could be explained by a downward migration during December and January, resulting in the introduction of limpets from higher levels into the low-level sampling zone.

Vertical migrational movements during the winter have been reported for *Acmaea digitalis* by Frank (1965) at Coos Bay, Oregon and by Breen (1972) at Port Renfrew, British Columbia. Instead of migrating downward during the winter, as suggested here for *A. strigatella, A. digitalis* migrated upward. This upward movement occurred at a time when increased wetting of the high intertidal zone took place as a consequence of increased wave splash. Lowered air temperatures and coastal fog during the winter months also favor extended periods of tidal exposure. Breen considered the occurrence of higher high tides during the day time and lower low tides between dusk and midnight in British Columbia to favor migration to higher levels. An explanation for the difference in direction of migration in the present study would appear to lie in the nature of the study site at Corona del Mar, rather than in the species concerned. The site (Figure 1) is unique in that it is protected from heavy surf (except when swells approach from the south) and the rocks and concrete wall from which the limpets were collected face 15° south of due west. This situation makes these limpets particularly susceptible to afternoon insolation. The time of day at which the lowest tides occur (and hence the longest periods of exposure to air) varies from month to month. Afternoon lower low tides are much more frequent in the winter than at other times (Table 1). The frequency of afternoon tidal exposure began to increase greatly during November and reached a peak in January and February. This phenomenon and the fact that the study site receives direct exposure to the sun in the after-

Table 1

Number of Days per Month When Minus Tides (Tidal Levels below 0.0 Datum) occurred during the Afternoon

Month	Number of Days
July (1970)	0
August	0
September	0
October	7
November	12
December	13
January (1971)	15
February	16
March	11
April	4
May	0
June	0

noon could account for the downward migration suggested to have taken place in January 1971.

During the month of May a mean upward movement of 17.2 cm was recorded (Figure 6). This upward migration may have been an anomalous situation for this time of year, because movement was possibly triggered by a stormy, overcast period observed during the first 2 weeks of May. Greatly increased wave splash was observed at this time.

The migration of *Acmaea strigatella* to lower levels during the summer months would have had to occur in early July in order to explain the data on extra-visceral space for the low-level sampling zone during the latter half of that month (Figure 5). Explanation of a slope of 0.457 for the low-level sampling zone requires the downward movement of limpets from higher levels. That such a downward migration could have occurred during early July is partially supported by the tidal pattern for this period of time (Figure 7). Four dates were selected here to illustrate the progressive occurrence of higher high tides at later times during the afternoon, accompanied by exposure of the intertidal region above about +1.2 m (= +4 ft.) during the preceding daylight hours. Plotted separately beneath the tidal curves for each date are records of air temperature and wind velocity taken at 3-hour intervals between 0400 and 1600 hrs (Orange County Harbor District records for Newport Bay, taken at a weather station located approximately 0.8 km north-northeast of the study site). Air temperature did not appear to be limiting by itself, as the maximum temperature attained during the first 10 days in July was only 23° C. Averaging the air temperature data over the 10-day period (Table 2), a stable pattern emerges of mild early morning temperatures (about 17° C at 0400 hrs) which rose only slowly during the day to about 21° C at 1600 hrs. An examination of data on wind velocity, however, suggests considerable variability between the 4 dates selected in Figure 7. This variability is also evident for the averaged

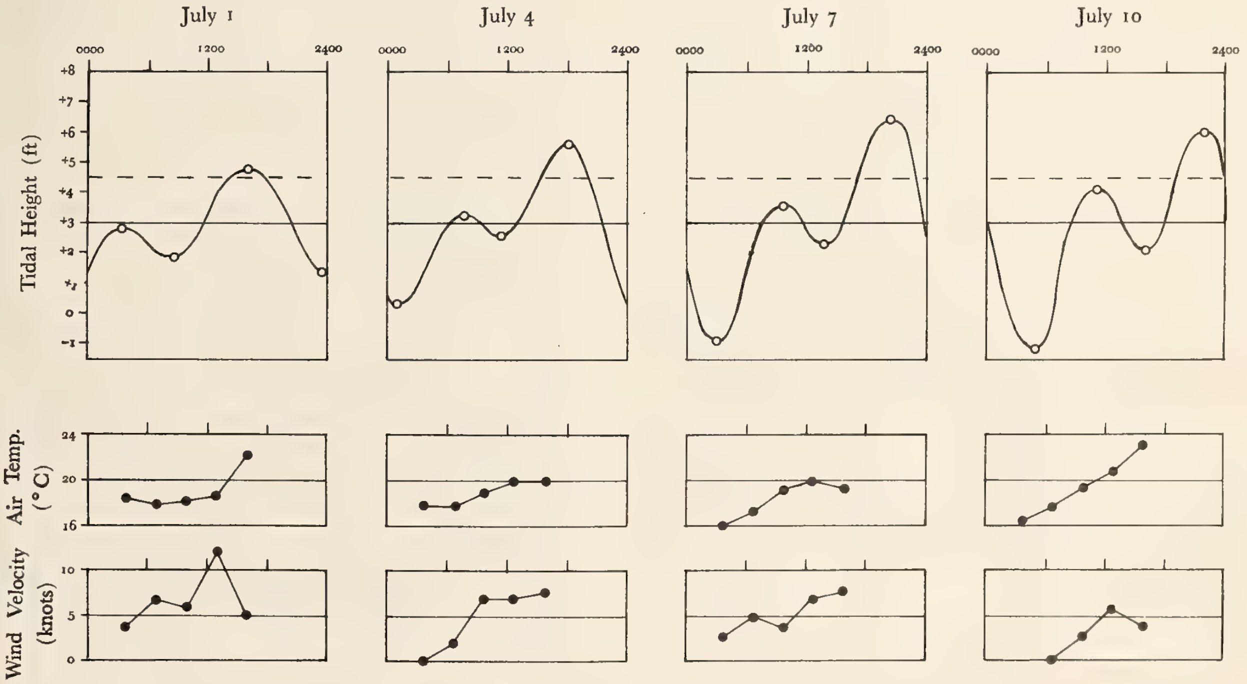

Figure 7

Tidal Curves for 1, 4, 7, and 10 July 1971 (constructed from tidal data for Los Angeles Harbor, 1971 Tide Tables, U. S. Department of Commerce, Air Temperatures and Wind Velocities at 3-hour Intervals (between 0400 and 1600 hrs) at Newport Harbor are included for each Date (see text for location of weather station).

Table 2

Averaged Air Temperatures and Wind Velocities at 3-hour Intervals between 0400 and 1600 hrs for 1 - 10 July 1971

	Time of Day (hrs)				
	0400	0700	1000	1300	1600
Averaged Air Temperature in °C [1]					
	16.95	17.40	18.94	19.77	20.94
	(0.66)	(0.57)	(0.80)	(1.08)	(1.14)
Averaged Wind Velocity in Knots [1]					
	2.20	2.50	4.50	8.10	6.60
	(2.56)	(2.41)	(2.06)	(2.26)	(1.62)

[1] N = 10, ( ) denotes one standard deviation

data over the 10-day period (Table 2). High standard deviations were recorded for each mean value and a maximal daily wind velocity of 6 to 10 knots occurred at 1300 hrs. A consistent feature of the 10-day period was the occurrence of southerly winds at 0400 hrs and progressive rotation of wind direction from the south to southwest by 1600 hrs. Thus, the morning and early afternoon exposure by the tides, coupled with warm air temperatures and a southerly to southwesterly breeze of up to 10 - 12 knots (in the afternoon) could have created sufficient desiccation stress in higher-level *A. strigatella* to induce the hypothesized downward movements. At some time during the fall months of 1971, limpets originally from higher levels would have had to migrate upward from the low-level sampling zone, if the November-December sample of 1970 is to be considered predictive for other years.

In the preceding discussion, we have made the assumption that vertical movements by *Acmaea strigatella* above about +1 m are affecting the specific composition of the low-level sampling zone in terms of extra-visceral space. Although the assumption would appear reasonable, it must be qualified since data on vertical movement below +1 m were not obtained.

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Diversity of Feeding Mechanisms among Embryos of Pacific Northwest *Thais*

BY

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(3 Text figures)

INTRODUCTION

Prosobranch embryos may hatch as veligers or may metamorphose in the capsule. These developmental strategies are associated with different types of embryonic food supply. The free-swimming veligers collect a variety of nanno- and microplanktonic cells with cilia on the velar edge and pass them to the mouth along the distinct food groove; algal cells 4 μm to 30 μm in diameter are the most frequently captured foods (Fretter & Montgomery, 1968). Embryos that do not feed in the plankton are provided with a large yolk supply, either within each egg, or externally, in the form of sterile "nurse eggs."

Embryos provided with nurse eggs must consume several of these "particles," each as large as the embryo itself, when the feeding begins, and each an order of magnitude larger (range 130 - 325 μm, Fioroni, 1966) than the typical foods of a free-swimming counterpart, to obtain its yolk. Such a task requires feeding mechanisms not possessed by the free-swimming larvae.

Three mechanisms have been described from observations on Muricacea. Eggs are swallowed whole by *Murex senegalensis* Gmelin, 1791, *M. quadrifrons* Lamarck, 1822, *M. incarnatus* (Röding, 1798), *Thais emarginata* (Deshayes, 1839), *T. hippocastaneum* (Lamarck), and *T. dubia* (Krauss) (Knudsen, 1950; Gohar & Eisawy, 1966; LeBoeuf, 1971; and Bokenheim & Neugebauer, 1938). The ingested eggs are visible as distinct bulges in the body wall, and will spill out intact from an embryo opened during the feeding period. The nurse eggs of *T. emarginata, T. hippocastaneum,* and *M. senegalensis* clump to form a mat. Those of *T. lapillus* (Linnaeus, 1758) also clump, but fall to pieces in the process, so the embryos consume only pieces of eggs (Thorson, 1946; Pelseneer, 1916). In the most different feeding method, a *Murex virgineus* Sowerby embryo manipulates a nurse egg with its velar lobes, collapses the egg by pressing on it with the lobes, and then sucks up the contents (Natarajan, 1957).

FEEDING of *Thais* EMBRYOS

The 4 Pacific Northwest species of *Thais* belong to the subgenus *Nucella,* and have many morphological and ecological features in common. Individuals form dense populations in the intertidal zone, where all feed readily on *Balanus glandula* Darwin, 1854 (Spight, 1972, and observations of R. T. Paine on *T. lima* (Gmelin, 1791) in the laboratory). Females attach their tough-walled egg capsules to intertidal rock surfaces; these open after 3 to 5 months and between 10 and 50 hatchlings emerge from each (the number varies with the capsule size, but in the same way for the 4 species; Spight, *op. cit.*). Despite the many characteristics common to these species, the embryos use 3 different means to obtain their yolk supplies.

A freshly deposited *Thais emarginata* capsule contains a few fertile eggs and many infertile nurse eggs. Emlen (1966) counted 300 to 1000 eggs (mean, 615; SD = 221) in capsules from Port Townsend, Washington. LeBoeuf (1971) counted 64 to 750 (mean about 500) eggs in others from California; of these 3 to 39 (mean, 16) developed.

The larvae begin ingesting the nurse eggs when the velar lobes are partially expanded (Figure 1). The nurse eggs are usually matted together when the embryos are feeding. The embryos grasp eggs on the outside of the mass and often cannot be detached without injury. The mouth, esophagus, and body expand to enclose the eggs as they are pushed down the digestive tract by the long cilia lining it. As each egg is swallowed, the body outline becomes more irregular, and often each embryo in a capsule has a unique shape (Figure 1). Embryos must be

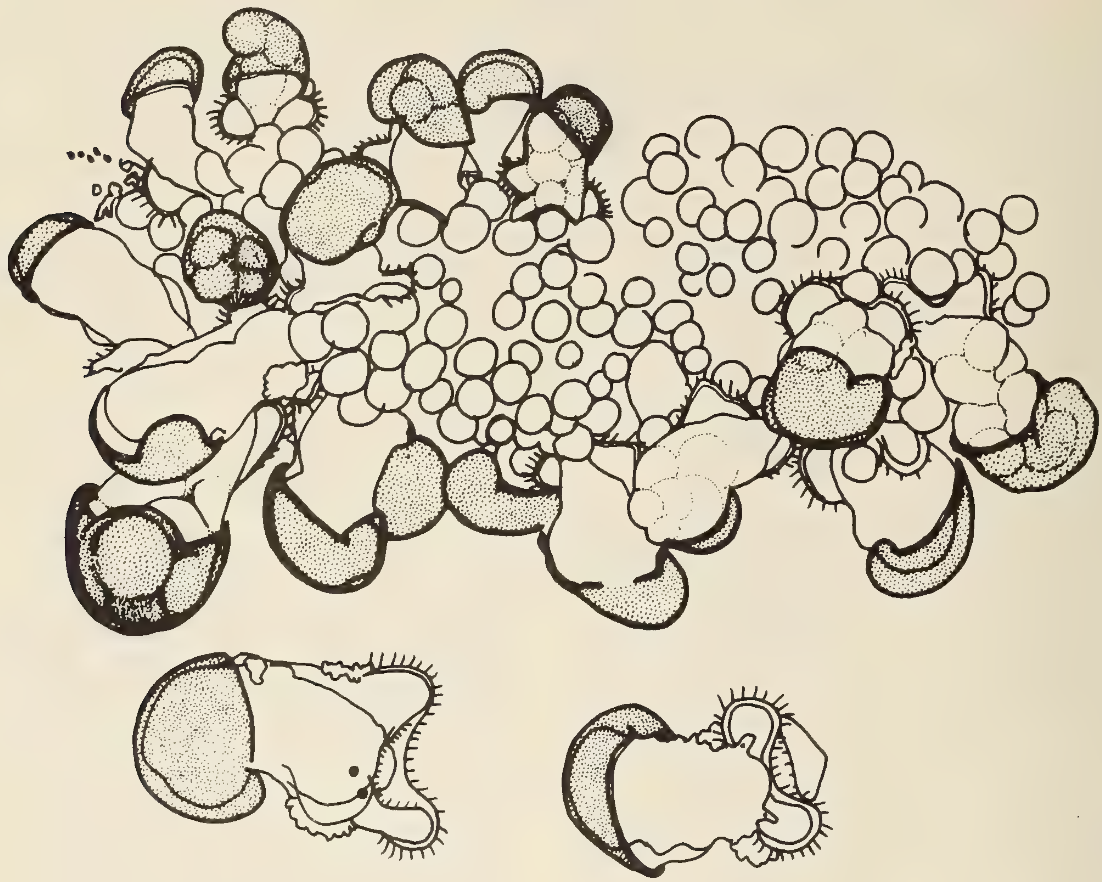

Figure 1

A matted mass of *Thais emarginata* nurse eggs removed from a capsule, with attached month-old veligers (two of the larger ones have fallen off the mass). The outlines of whole eggs can be seen through the transparent body wall of several veligers. The 4.2 mm long mass is from a capsule collected near Friday Harbor, Washington.

capable of feeding on intact nurse eggs for only a few days, since eggs not eaten at this time (*e. g.* when there are only 3 or 4 embryos in the capsule) will remain in the capsule until the end of the developmental period.

Thais canaliculata (Duclos, 1832) capsules may also contain nurse eggs. Houston (1971) counted between 200 and 300 eggs in freshly deposited capsules from California; 97% of these were nurse eggs. Capsules about the same size (1 cm long) collected on San Juan Island, Washington, contained about a tenth as many eggs, and most of these were fertile (the mean egg count in samples taken at the beginning and the end of the developmental period did not decrease significantly; Spight, 1972). However, the single San Juan Island female that has oviposited in the laboratory placed infertile eggs in all of the 18 capsules we opened, and among 5 capsules with prefeeding veligers, 16% to 92% of the eggs were developing.

The feeding method of the *Thais canaliculata* embryos was unique. An embryo grasped a nurse egg with the cilia in the dense patches on the front of the head and the propodium (Figure 2) and rotated it until pieces flaked off. The infertile eggs did not clump.

Infertile *Thais lamellosa* (Gmelin, 1791) eggs are rare. The embryos (Figure 3) have neither the expansible mouth and esophagus, nor the very large cilia lining mouth and esophagus or head and propodium, used by the other species for manipulating and ingesting nurse eggs. The few infertile eggs remain intact in the capsule through the developmental period, and are unavailable to the embryos (we assume they will be broken apart with the radula just prior to hatching).

Thais lima females maintained in a 10° C cold room by R. T. Paine deposited a few capsules in the fall of 1971. All of the eggs in the capsules opened were developing. The embryos were not examined in detail.

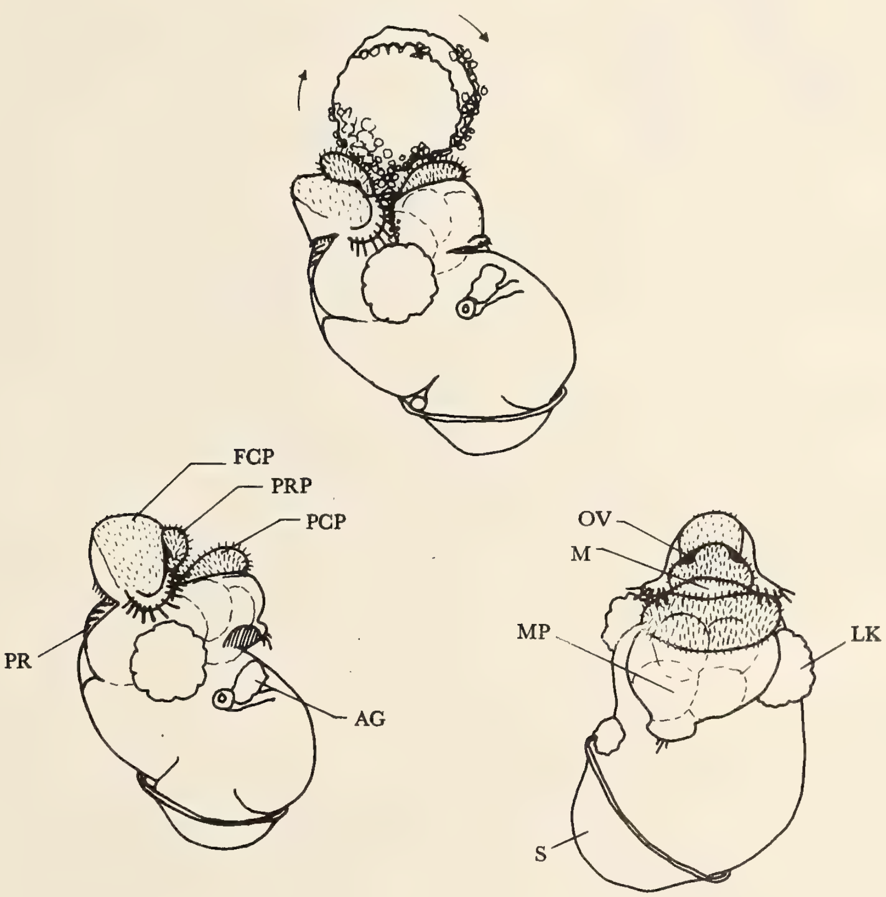

Figure 2

A *Thais canaliculata* veliger feeding on an infertile egg. The front of the head (PRP, preoral ciliary patch) and propodium of the foot (PCP, propodial ciliary patch) were heavily ciliated. The veliger rotated the egg over the mouth with these cilia until pieces of the egg were torn off. This veliger was removed from a capsule 31 days after it was deposited in an aquarium with running seawater (temperature 12° C). The velar lobes are not as expanded as those of *Thais emarginata* or *Thais lamellosa* veligers of the same age.

AG – anal gland; FCP – frontal ciliary patch; LK – larval kidney; M – mouth; MP – metapodium; OV – optic vesicle; PR – larval heart; S – shell

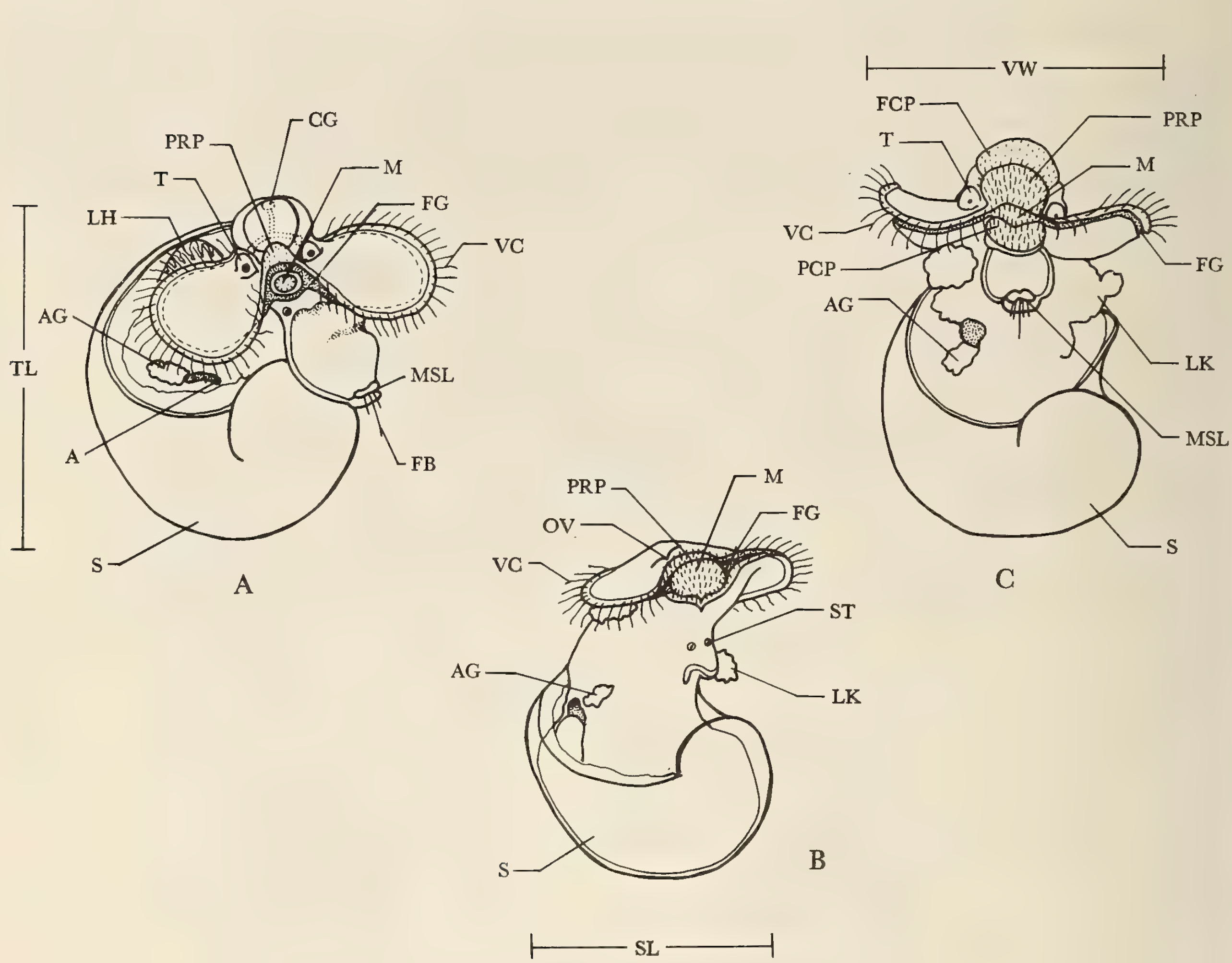

Figure 3

Month-old embryos of three Northeast Pacific *Thais* species. Capsules were deposited in aquaria with running seawater on 3 May by *Thais emarginata* (B) and *Thais canaliculata* (C) females, and on 5 May by *Thais lamellosa* (A) females; all were opened on 10 June. Temperature 12°C. The VELAR LOBES are flat from the sides of the head, and joined by the pre-oral ciliary patch (PRP), which is prominent in C. The vela of C are fleshier and inflatable. The head area of B is flat; the velar lobes rest on thick stalks, so only the edge is free, and the organ has a correspondingly smaller range of movement. The FOOD GROOVE is well-developed in A and C, but represented only by a wedge-shaped patch of cilia at the sides of the mouth and a narrow groove along the front quarter of the velum in B. The cilia in the mouth and esophagus are much denser and longer in B. The TENTACLES are well-developed with a prominent eyespot in A, thick and rounded in C, but represented only by an optic vesicle (OV) in B. On the FOOT, the operculum is present, and the statocysts are prominent in A and B. Propodium and metapodium are differentiated and there is a metapodial sensory lobe with bristles in A and C. The propodium is densely covered with large cilia used for turning nurse eggs in C.

Measurements (in μm)

	(VW)	(SL)	(TL)
Thais lamellosa (A)	660	690	750
Thais emarginata (B)	620	720	660
Thais canaliculata (C)	780	660	1000

(VW) – velum width; (SL) – shell length; (TL) – total length

A – anus; AG – anal gland; CG – cerebral ganglion; FB – foot bristles; FCP – frontal ciliary patch; FG – food groove; LH – larval heart; LK – larval kidney; M – mouth; MSL – metapodial sensory lobe; OV – optic vesicle; PCP – post-oral ciliary patch; PRP – pre-oral ciliary patch; S – shell; ST – statocyst; T – tentacle; VC – velar cilia

FEEDING AND DEVELOPMENTAL SEQUENCE

These embryonic feeding mechanisms are operable for only a brief period early in the developmental sequence; the *Thais emarginata* embryos expanded from 290 μm to 1000 μm within 10 days. The older embryos are similar to the free-living veligers, and, like them, are incapable of ingesting large particles.

Older embryos will readily capture small particles available to them with the velar cilia, transport them through the food groove, and ingest them. The major source of particles in a closed capsule is the decomposition of infertile eggs and dead capsule mates. Embryos do not tolerate heating or dehydration, and will be killed if a capsule is exposed directly for a single low tide (SPIGHT, 1972). A few of the embryos from each capsule will die during the 3-month developmental period, and will then decompose and provide food for their living capsule mates.

The feeding of *Thais emarginata* has been described in older works (*e. g.*, JOHNSON & SNOOK, 1927) as "cannibalism." Although some embryos may be consumed by others during the feeding period, all of the encounters we have seen have been peaceful. Older veligers are not capable of killing their fellows and feed on dead fellows only after these decompose to small particles. Feeding on nurse eggs or on dead fellows is "cannibalism" in only the most literal sense. We know of no observations of any muricacean embryos killing their capsule-mates.

EVOLUTIONARY SIGNIFICANCE

Embryos of 5 species have been observed while feeding on nurse eggs, but only 2 of them utilized the same technique. The differences do not correspond with present taxonomic divisions; the 3 members of the subgenus *Nucella* in the group use 3 different means (and the 2 additional Northwest members do not feed on nurse eggs). Mechanisms for feeding on nurse eggs must have evolved independently several times.

The type of embryonic food supply (yolk, nurse eggs, or planktonic algae) used by members of a single species also varies from place to place. Nurse eggs are the major food source for *Thais canaliculata* from California (HOUSTON, 1971), but each egg has its own yolk supply at Friday Harbor. *Thais haemastoma* (Linnaeus, 1758) at some localities feed on nurse eggs and metamorphose in the capsule; at others, all of the eggs are fertile and hatch as free-swimming veligers (THORSON, 1950).

Embryonic food supply is a characteristic that can vary to suit local conditions. The members of the group (Muricacea) are sufficiently variable that it may be possible to determine the precise selective factors that favor planktonic larvae at some localities and direct development at others.

SUMMARY

Muricacean embryos utilize a variety of methods to obtain their yolk supply. Closely related species (*e. g.*, the 4 Northwest *Thais*) may utilize different methods. Geographically separated races of the same species may also utilize different methods; for example, *Thais canaliculata* embryos from California obtain most of their yolk by consuming nurse eggs, while those from Washington do not. Mechanisms for ingesting nurse eggs are operable only during a short period early in the developmental sequence; no older embryos of any species can ingest such large particles.

ACKNOWLEDGMENTS

We thank R. L. Fernald for making the facilities at Friday Harbor Laboratories available to us. The viewpoint of the paper was suggested in a conversation with R. Strathmann. The study was supported by NSF Grant GB 6518X.

NOTE ADDED IN PROOF:

We were unable to find specimens of *Thais canaliculata* at Nick's Cove in June, 1972. HOUSTON's (1971) description of capsules and adults found at this site are compatible with our observations on the *T. emarginata* population there and differ markedly from our observations on *T. canaliculata* in Washington.

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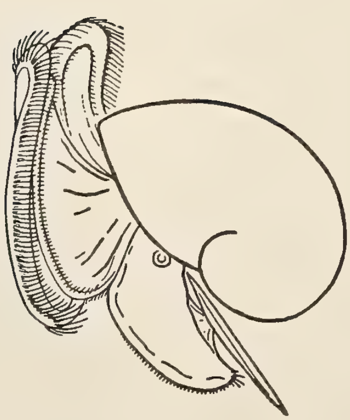

Seasonal Changes in the Body Component Indices of the Subtidal Prosobranch *Fusitriton oregonensis*

BY

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(2 Text figures)

INTRODUCTION

SEASONAL CHANGES IN SEVERAL BODY component indices of the intertidal prosobranch *Thais lamellosa* (Gmelin, 1791) were related to prey availability (STICKLE, 1973). EMLEN (1966) has shown the ability of *T. lamellosa* to prey upon the barnacles *Balanus glandula* Darwin, 1854 and *B. cariosus* Pallas, 1788 to be related to both barnacle size and position in the intertidal zone. The snails feed only when submerged and are not submerged long enough to drill through large *B. glandula* located high in the intertidal zone (CONNELL, 1970). The large barnacles in the narrow "refuge" zone at the top of the intertidal zone produce enough young to repopulate the intertidal zone each spring. Young barnacles are eliminated by predation in all but the "refuge" zone by late autumn.

One way of evaluating the effect of prey availability upon nutrient accumulation of predators would be to study seasonal changes in the body components of a species which has adequate supply of prey year around. The subtidal prosobranch *Fusitriton oregonensis* (Redfield, 1848) was chosen because of its generalized feeding habits and large size which makes it possible to dissect many components from the soft parts.

Fusitriton eats a variety of invertebrates including echinoids, ascidians, amphineurans, prosobranchs, and pelecypods. The most active feeding period is at night. The green sea urchin, *Strongylocentrotus drobachiensis* (O. F. Müller, 1776) was observed to be the most common prey of *F. oregonensis* in the field (EATON, 1971). The species has been observed scavenging, perhaps as a result of having killed its prey the night before. An ample food supply is probably always available to these snails.

Fusitriton oregonensis is found on the west coast of North America from Alaska to Mexico. The species rarely occurs in the intertidal zone but is found in considerable numbers in 2 m to at least 180 m depth.

Fusitriton oregonensis is one of the most advanced mesogastropods. It has a well developed reproductive system with which it deposits its eggs in capsules which look like kernels of corn. Egg capsules are usually laid on rock surfaces and when females are uncrowded, the capsules are arranged in a circular egg mass of up to 100 capsules (EATON, 1971; HOWARD, 1962).

The reproductive behavior of *Fusitriton oregonensis* has been documented by EATON, 1971. Pair formation begins approximately 6 months prior to egg laying. Egg laying begins in June or July and is signalled by a behavioral change of females which remain on the breeding aggregation during the day instead of in crevices or at the bases of rocks. If males are found near the aggregation they are located around its periphery. Females normally brood the eggs from the time the capsules are laid until the last one has hatched 8 - 9 weeks later. Eaton found this brooding behavior to prevent capsule predation.

METHODS AND MATERIALS

Fusitriton oregonensis were periodically collected from April 24, 1969 to June 5, 1970 at Edwards Reef off the west coast of San Juan Island, Washington. Collections were made with SCUBA gear in 10.6 to 18.3 m of water. Field observations were made by Stickle through August 1969. After being taken to the Friday Harbor Laboratories, animals were frozen and then shipped to Slippery Rock State College for analyses.

Component Indices: - Animals were thawed, the outer shell blotted dry, and the entire animal was weighed. The

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shell and operculum were removed, and excess water was wiped from the soft tissue before it was weighed. The animals were then sexed and separated into the following soft body components: gonad-digestive gland, capsule-albumin gland or penis, kidney, mantle, foot and remaining visceral mass. The foot was dissected from the remainder of the parts by cutting along a line from just in front of the 2 tentacles to the posterior edge of the opercular scar. The gonad-digestive gland, kidney, mantle, capsule-albumin gland, and remaining visceral mass components were dissected free in their entirety. The penis was dissected free at its base. The soft components were dried to constant weight at 90 - 100° C. Body component indices were calculated as in an earlier study (STICKLE, 1973). Each index was expressed as grams of the component per grams of the entire animal times 100.

Statistical Analyses - All data are given as the mean ± the 95% Confidence Interval.

RESULTS

Field Observation - *Fusitriton oregonensis* were scattered in the study area on June 2, 1969. One female was observed to be laying eggs on July 1, and many females were aggregated and laying cases on July 22. Animals were still aggregated when collected on August 23. No males were found among the animals collected on July 22 and August 23.

Component Indices - Female kidney, mantle, foot, shell, and body water index data are given in Table 1. No seasonal pattern was observed with respect to changes in the magnitude of any of these indices. An inverse relationship existed between the shell and body water indices throughout the study.

Data for the female ovary-digestive gland and capsule-albumin gland indices are depicted in Figure 1. The termination of the breeding aggregation was estimated to be about September 15 by using EATON's (1971) estimate of an 8 - 9 week developmental period for the embryos. The ovary-digestive gland index declined from an average June 2 value of 4.83 to 2.85 on August 23. This index did not reach the same magnitude in 1970 that it did in 1969. The capsule-albumin gland index exhibited a distinct seasonal pattern. It declined from 1.96 on July 1 to 0.68 on August 23. The capsule-albumin gland index increased to near its 1969 prespawning magnitude by May 1970.

Remaining visceral mass index data are depicted in Figure 2. Highest levels were found in April, January, and February. A sharp drop occurred in the index between April and June 1969, which was not repeated in 1970.

The average index of each female body component exhibited the following seasonal range: kidney, 0.29 - 0.37; mantle, 0.43 - 0.62; foot, 1.16 - 1.46; capsule-albumin gland, 0.68 - 1.96; remaining visceral mass, 2.77 - 3.82; ovary-digestive gland, 2.85 - 6.02; body water, 25.55 - 30.28; and shell, 57.66 - 65.31.

Male kidney, mantle, foot, penis, testis-digestive gland, body water, and shell index data are given in Table 2. No seasonal pattern was observed in the magnitude of any of these indices. An inverse relationship existed between the body water and shell indices throughout the study.

Table 1

Seasonal Body Component Indices of Female *Fusitriton oregonensis*
g x 100g Animal^{-1} x 100

Date	Sample Size	Kidney	Mantle	Foot	Body Water	Shell
24/ IV/1969	9	0.36±0.03 [1]	0.62±0.10	1.41±0.11	29.10±2.06	57.66±3.03
2/ VI/1969	11	0.31±0.05	0.48±0.07	1.25±0.11	25.55±1.38	62.90±1.79
1/ VII/1969	6	0.33±0.05	0.50±0.16	1.15±0.15	27.64±2.32	60.63±2.03
22/ VII/1969	28	0.38±0.03	0.43±0.03	1.31±0.06	28.97±0.82	61.61±1.00
23/VIII/1969	24	0.37±0.04	0.43±0.02	1.34±1.28	26.14±0.86	65.31±0.84
10/ X/1969	8	0.29±0.08	0.55±0.12	1.34±0.10	26.55±1.97	63.74±3.47
16/ XI/1969	15	0.31±0.05	0.52±0.10	1.46±0.11	28.95±2.26	60.15±1.34
24/ I/1970	6	0.29±0.05	0.45±0.10	1.17±0.08	30.28±1.64	58.97±3.41
20/ II/1970	11	0.30±0.06	0.52±0.08	1.38±0.15	29.61±1.08	59.50±2.03
19/ III/1970	10	0.27±0.04	0.49±0.07	1.23±0.08	28.61±1.67	61.27±2.71
6/ V/1970	10	0.35±0.06	0.50±0.07	1.20±0.10	28.32±1.35	60.18±2.11
5/ VI/1970	7	0.29±0.04	0.49±0.08	1.16±0.16	28.16±1.81	61.11±3.68

[1] Mean ± 95% confidence interval

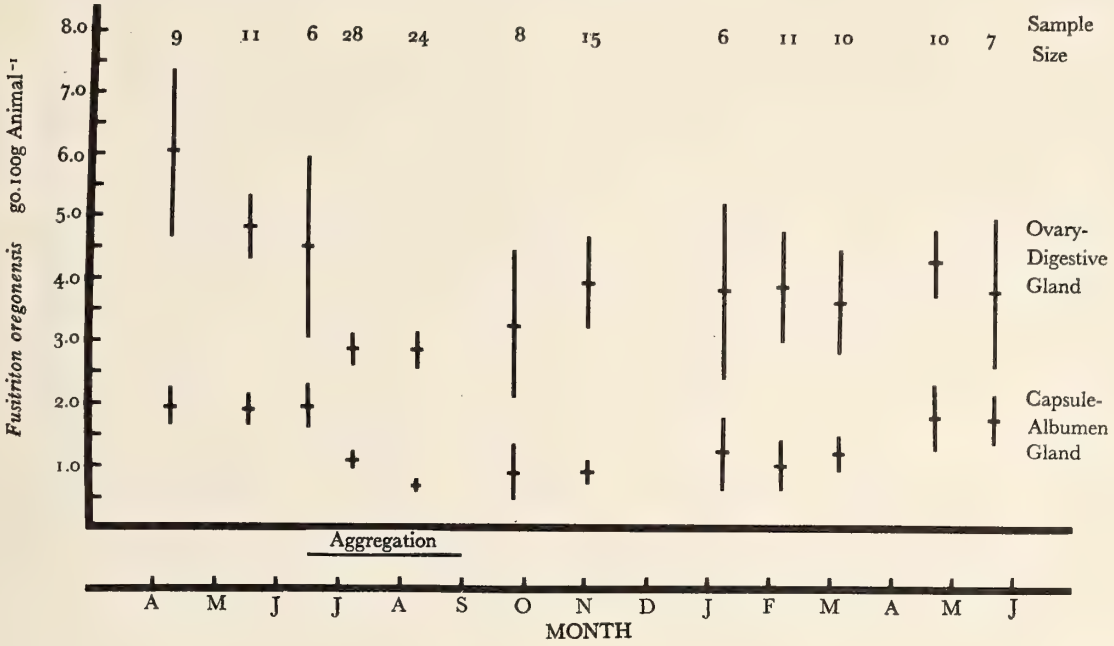

Figure 1

Female ovary-digestive gland and capsule-albumin gland indices are represented by crosses. The horizontal line of each cross represents the mean and the vertical line the 95% confidence range about the mean.

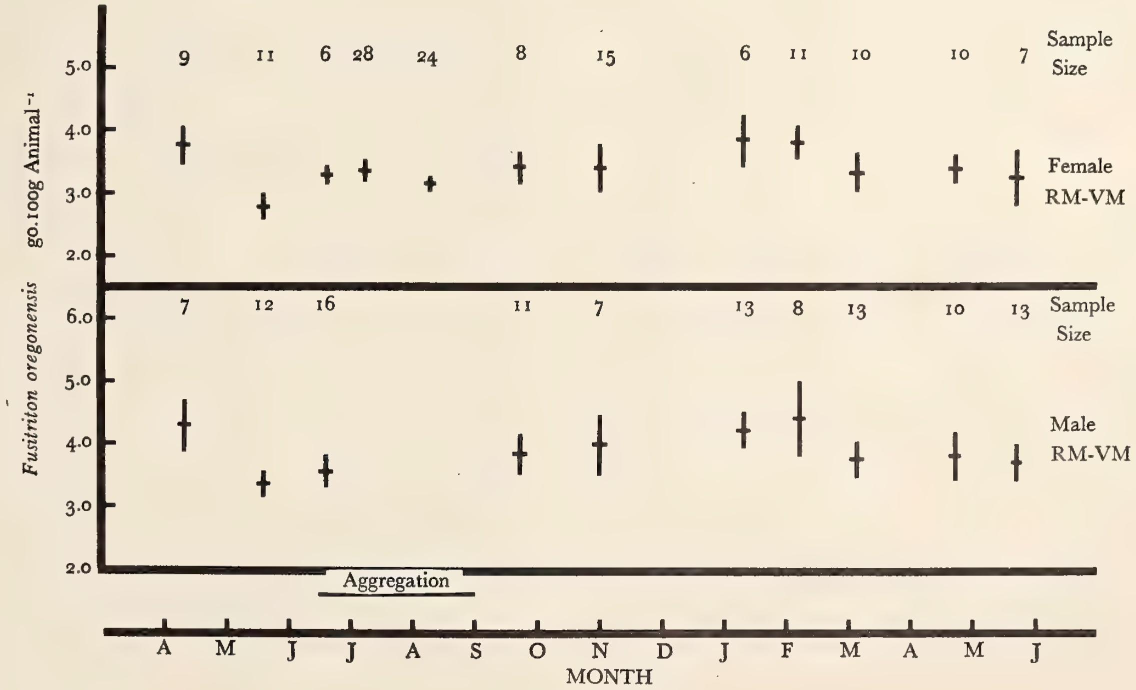

Figure 2

Remaining visceral mass indices of both sexes are represented by crosses. The horizontal line of each cross represents the mean and the vertical line the 95% confidence range about the mean.

Table 2

Seasonal Body Component Indices of Male *Fusitriton oregonensis*
g x 100 g Animal^{-1} x 100

Date	Sample Size	Kidney	Mantle	Foot	Penis	Body Water	Shell
24/ IV/1969	7	0.36±0.07 [a]	0.69±0.07	1.60±0.09	0.45±0.04	29.16±1.74	59.31±2.38
2/ VI/1969	12	0.32±0.04	0.53±0.08	1.53±0.14	0.42±0.04	25.57±1.53	64.64±2.20
1/ VII/1969	16	0.28±0.03	0.59±0.06	1.32±0.09	0.40±0.04	27.56±1.49	63.24±1.89
22/ VII/1969	0	....	....	....	....	....	....
23/VIII/1969	0	....	....	....	....	....	....
10/ X/1969	11	0.26±0.04	0.57±0.08	1.50±0.14	0.42±0.06	28.89±1.71	60.62±2.62
16/ XI/1969	7	0.33±0.08	0.61±0.09	1.65±0.25	0.43±0.07	29.24±1.25	59.96±2.03
24/ I/1970	13	0.30±0.03	0.56±0.08	1.42±0.09	0.43±0.06	28.97±1.95	60.35±2.44
20/ II/1970	8	0.32±0.05	0.59±0.10	1.39±0.15	0.41±0.05	28.46±2.37	60.81±3.38
19/ III/1970	13	0.24±0.02	0.53±0.05	1.37±0.12	0.40±0.07	28.32±1.44	62.40±2.02
6/ V/1970	10	0.26±0.04	0.63±0.12	1.35±0.09	0.39±0.08	28.32±1.10	62.15±1.74
5/ VI/1970	13	0.29±0.04	0.67±0.08	1.36±0.12	0.43±0.05	28.96±1.57	61.21±2.34

[a] Mean ± 95% confidence interval

Male remaining visceral mass index data are given in Figure 2. The same seasonal pattern was observed with the male remaining visceral mass index as was observed with the female component.

The average index of the male body components exhibited the following seasonal range: kidney, 0.24 - 0.36; penis, 0.39 - 0.45; mantle, 0.53 - 0.69; foot, 1.32 - 1.65; remaining visceral mass, 3.58 - 5.40; testis-digestive gland, 2.93 - 4.14; body water, 25.57 - 29.24; and shell, 59.31 to 64.64.

DISCUSSION

The female ovary-digestive gland and capsule-albumin gland indices of *Fusitriton oregonensis* and *Thais lamellosa* exhibited a distinct seasonal cycle. Indices for both components were larger for *F. oregonensis* and the indices declined more on an absolute basis than for *T. lamellosa* during spawning. However, the fact that the shell index is much larger in *T. lamellosa* than in *Fusitriton* probably explains the difference in the magnitude of the respective indices.

About the same percentage of the prespawning capsule-albumin gland index remained at the completion of spawning for the two species: 35% for *Fusitriton,* and 27 - 30% for *Thais.* However, 59% of the prespawning ovary-digestive gland index remained at the completion of spawning for *Fusitriton* as compared to only 26 - 33% for *T. lamellosa.* Biomass was lost from the ovary-digestive gland for both species as a result of spawning and catabolism by the female during aggregation. Aggregation was more than a month longer for *T. lamellosa* than for *F. oregonensis.* In addition, more biomass must be deposited per embryo of *T. lamellosa* than for *F. oregonensis* because development is completed in the capsule of *Thais,* but a free swimming veliger is released from the egg capsule of *Fusitriton.* It is impossible to estimate the total biomass lost by female *Fusitriton* for the production of spawn because there are no data available on egg or egg capsule production per female. Such data do exist for *T. lamellosa* (Spight, 1972) and Stickle (1973) has made the necessary calculations.

No body component of male *Fusitriton oregonensis* exhibited a seasonal cycle. In contrast, the testis-digestive gland index of *Thais lamellosa* exhibited a distinct seasonal cycle (Stickle, 1973). However, *T. lamellosa* males accompany the females to the breeding aggregations where copulation occurs. Males copulate and starve for the better part of the 3 to 4 month aggregation period. Pair formation occurs approximately 6 months prior to egg laying in *F. oregonensis* (Eaton, 1971). Copulation is intermittent and begins 4 months prior to egg laying. Eaton observed the percentage of *F. oregonensis* to be paired at Edwards Reef as follows: April - 43%, May - 62%, and June - 38%. The duration of individual pairs in the laboratory was highly variable. Many lasted only 1 or 2 days, while others remained together for as long as

28 days. Eaton states that there is a good chance that pairs found in nature are of a generally longer duration. This study indicates that male *F. oregonensis* feed often enough during the 4-month copulatory period to replenish biomass lost from the testis-digestive gland through copulation and respiration.

The decline in the remaining visceral mass index of both sexes between April and June 1969 cannot be explained at this time. The proboscis and salivary glands of *Fusitriton* account for much of the biomass of the remaining visceral mass. Seasonal changes in the size and physiology of gastropod salivary glands are in need of investigation.

The body components of *Fusitriton oregonensis* more closely resemble those of *Thais lamellosa* (Stickle, 1973) than those of *Haliotis cracherodii* Leach, 1814 (Giese, 1969; Webber & Giese, 1969; Webber, 1970), *Megathura crenulata* (Sowerby, 1825), or *Polinices lewisii* (Gould, 1847) (Giese, *op. cit.*). However, the reproductive behavior of *F. oregonensis* is much different from that of *T. lamellosa.* This fact is responsible for some of the differences in the pattern of biomass accumulation observed between males of the two species.

Differences in prey availability do not effect the similar pattern of biomass accumulation in the reproductive tract of female *Thais lamellosa* and *Fusitriton oregonensis.* However, differences in the biochemical characteristics of the reproductive tract of the two species may account for the different chemical composition of the respective egg capsules. The egg capsules of *T. lamellosa* are composed of 51% protein, 13% lipid, and 2% polysaccharide as compared to 24% protein, 11% lipid, and 2% polysaccharide in *F. oregonensis* egg capsules (author's unpublished data). Protein must be accumulated in much higher concentrations in the reproductive tract of *T. lamellosa.*

SUMMARY

1. Body component indices of *Fusitriton oregonensis* were determined over a period of 15 months. Snails were separated into shell, body water, gonad-digestive gland, capsule-albumin or penis, kidney, mantle, foot, and remaining visceral mass. Indices were expressed as grams of the component per gram of the entire animal times 100.

2. The female ovary-digestive gland and capsule-albumin gland indices exhibited a distinct seasonal cycle of being largest in the several months prior to aggregation, declining during that period, and increasing several months prior to the next aggregation.

3. No body component of the males exhibited a seasonal cycle. Males apparently feed often enough during the 4-month copulatory period which precedes aggregation to replenish biomass lost through copulatory activity. No males were collected from the breeding aggregation.

4. It does not appear that seasonal differences in prey availability are responsible for the accumulation of biomass in the reproductive tract of female *Fusitriton oregonensis* during the several months prior to aggregation. It is likely that some endogenous factor is responsible for this fact.

ACKNOWLEDGMENTS

The authors wish to thank Dr. Gordon Robilliard for collecting animals for us from September, 1969 to June, 1970. This research was partially funded by a National Research Council of Canada research assistantship granted to W. B. S. and in part by S. R. S. C. Biology funds.

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Type Specimens of Mollusca from the Charles R. Orcutt Collection Now at the University of California, Riverside

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In 1958 the portion of the Charles R. Orcutt mollusk collection previously housed at Pomona College, Claremont, California, was acquired by the Department of Geological Sciences, University of California, Riverside. The existence of this part of the pioneer Californian conchologist's extensive collection has apparently not been known to molluscan specialists (Coan, 1966). Numbering over 33 000 specimens, the collection consists in about equal proportions of both marine and nonmarine Mollusca.

During a recent reorganization of the collection, I located 48 primary type specimens, 1 bivalve and 47 gastropods. These specimens have been placed in the type collection of the Department of Geological Sciences and bear the numbers recorded below.

BIVALVIA

Chlamydoconcha orcutti Dall
 Dall, 1884: 51
 Syntype 7258/9850; Mission Bay, San Diego, San Diego County, California

GASTROPODA

Ashmunella danielsi Pilsbry & Ferriss
 Pilsbry & Ferriss, 1915b: 34
 Paratype 6632/1; Cave Spring Canyon, Mogollon Mountains, Socorro County, New Mexico

Ashmunella tetrodon Pilsbry & Ferriss
 Pilsbry & Ferriss, 1915a: 15
 Paratype 6631/1; Dry Creek Canyon, Mogollon Mountains, Socorro County, New Mexico

Caecum orcutti Dall, *in* Orcutt, 1885
 Orcutt, 1885: 541
 Syntypes 6659/1, 6659/2, 6659/3, 6659/4, 6659/6347; San Diego, San Diego County, California

Cerion (Strophiops) biminiense Henderson & Clapp
 Henderson & Clapp, 1913: 64
 Paratype 6685/1; North Bimini Island, Bahamas

Cylindrella atropurpurea Arango
 Arango, 1882: 106
 Syntype 6611/6054; near La Palma, Pinar del Rio, Cuba

Cylindrella hidalgoi Arango
 Arango y Molina, 1878: 107
 Syntypes 6610/1, 6610/4405; Pinar del Rio, Cuba

Cylindrella incerta Arango
 Arango, 1881: 15
 Syntype 6612/3619; Puerta de la Muralla, Cuba

Diplommatina dohertyi Godwin-Austen
 Godwin-Austen, 1892: 513
 Syntypes 6617/1, 6617/2; Margarita, Naga Hills, Assam, India

Epiphragmophora orcutti Dall
 Dall, 1900: 104
 Syntype 6608/7103; El Rosario mesas, northern Baja California, Mexico

Epiphragmophora (Trichodiscina) verdensis Dall
 Dall, 1910: 35
 Paratype 6619/6302; Rio Verde, Oaxaca, Mexico

Eucalodium (Anisospira) orcutti Dall
 Dall, 1910: 34
 Paratypes 6619/1, 6619/3873; Rio Verde, Oaxaca, Mexico

Gonyodiscus clappi Pilsbry
PILSBRY, 1925: 417
Paratype 6607/1; Jasper Point, 4 miles north to northeast of Gurley, Madison County, Alabama

Haliotis bonita Orcutt
ORCUTT, 1900: 30
Paratype 6641/9411; Baja California, Mexico

Haliotis rosea Orcutt
ORCUTT, 1900: 30
Paratype 6634/9414; ?San Diego, San Diego County, California

Holospira pasonis Dall
DALL, 1895: 112
Paratype 6622/8247; Mule Canyon, El Paso County, Texas

Leptinaria livingstonensis Hinkley *in* Pilsbry, 1920
PILSBRY, 1920: 213
Syntypes 6613/1, 6613/6952; Livinston, Guatemala

Macron orcutti Dall
DALL, 1918: 5
Paratype 6640/10193; Magdalena Bay, Baja California, Mexico

Marginella californica parallela Dall
DALL, 1918: 6
Paratypes 6640/1, 6640/2, 6640/3, 6640/4, 6640/10185; Magdalena Bay, Baja California, Mexico

Oreohelix pilsbryi Ferriss
FERRISS, 1917: 102
Paralectotypes 6630/1, 6630/2; near Chloride, Sierra County, New Mexico

Oreohelix (Radiocentrum) hachetana Pilsbry
PILSBRY, 1915: 330
Paratype 6627/1; summit of Hacheta Grande Mountain, Hidalgo County, New Mexico

Polygyra brevipila cherokeensis Clapp
CLAPP, 1916: 3
Paratype 6623/9424; near Pleasant Gap, Cherokee County, Alabama

Polygyra cohuttensis Clapp
CLAPP, 1914: 78
Paratype 6625/9445; Fort Mountain, Murray County, Georgia

Polygyra decepta Clapp
CLAPP, 1905a: 25
Paratype 6606/9447; Blount Springs, Blount County, Alabama

Polygyra inflecta approximans Clapp
CLAPP, 1905b: 74
Paratype 6605/9420; near Marion, Perry County, Alabama

Polygyra pseudodonta Dall
DALL, 1897: 343
Paratype 6626/5207; White Oaks, Lincoln County, New Mexico

Polygyra smithii Clapp
CLAPP, 1905b: 73
Paratypes 6604/1, 6604/9421; Monte Sano, near Huntsville, Madison County, Alabama

Polygyra (Stenotrema) barbata Clapp
CLAPP, 1904: 85
Syntype 6624/1; Tallapoosa River about 5 miles southeast of Wetumpka, Elmore County, Alabama

Punctum conspectum pasadenae Pilsbry
PILSBRY, 1896: 21
Paratypes 6603/1, 6603/6996; Pasadena, Los Angeles County, California

"Pyramidula" strigosa huachucana Pilsbry
PILSBRY, 1902: 511
Paratype 6629/1; Conservatory Canyon, Huachuca Mountains, Cochise County, Arizona

Sonorella hatchitana flora Pilsbry
PILSBRY, 1915: 347
Paratype 6628/1; Florida Mountains, Luna County, New Mexico

Sonorella rooseveltiana Berry
BERRY, 1917: 14
Paratypes 6609/1, 6609/10586; Roosevelt, Gila County, Arizona

In addition, there is one specimen in the collection labeled "*Bulimus lhotelleri* Bourg. (types) 3602." I have not as yet found the appropriate literature to verify the authenticity of this species.

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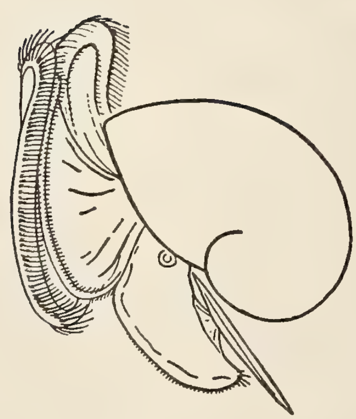

Aboral Extrusion of Squid Pens by the Sea Star *Pycnopodia helianthoides*

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(2 Plates; 1 Text figure)

INTRODUCTION

THE BREAKING OF the aboral body wall of the sea star *Astropecten californicus* Fischer, 1906, which swallowed a large bivalve, *Donax vittatus* da Costa, 1789, is mentioned by CHRISTENSEN (1970: 58). Christensen assumed the breakage was due to the sea star being washed ashore and left to dry in the sun during low tide. Since previous reports had been based on dead and, in most cases, dried specimens, Christensen was convinced that fissures in body walls of these sea stars were of post mortal origin.

After spawning, dead and dying squid, *Loligo opalescens* Berry, 1911, are found in great numbers on the floor of Monterey Bay, California. Many of these spent animals become a temporary part of the diet of the sea star *Pycnopodia helianthoides* (Brandt, 1835).

In April, 1971, on the seaward side of the United States Coastguard Breakwater at the southwest end of Cannery Row, Monterey, California, a *Pycnopodia helianthoides* was found subtidally with the anterior end of the pen (or shell) of a *Loligo opalescens* protruding 3 cm out through its aboral surface. The pen was 8 cm distant from the madreporite, and it was not through the sea star's anus. Two of the sea star's rays were up over the disc, wrapped around the pen. When the pen was extracted, a white, fleshy substance, presumed to be partly digested squid material, came out of the slit.

An experimental feeding in the field of 20 to 30 fresh market *Loligo opalescens* to individual *Pycnopodia helianthoides* resulted in the observation of only one sea star with a squid pen protruding 5 cm through its aboral surface. Since the fed sea stars were unmarked, some may have moved out of sight beneath the rocks. A *P. helianthoides* fed a squid in the laboratory did not put the whole animal into its stomach as did sea stars in the field. An experiment was devised to determine whether *P. helianthoides* typically eliminates squid pens in the field by forcing them through its aboral surface.

METHODS

Five isolation containers for a series of subtidal tests were constructed from round plastic baskets tied together (Figure *1*). Each basket was 37 cm in diameter and 26.6 cm deep. A galvanized pipe was fastened to the baskets and served as a base. The baskets were covered with fine-mesh plastic screen to keep non-test sea stars from reaching into the baskets for squid (as was the case on the first test, run without the screen). Lids were pressed into the slightly tapered baskets. The isolation containers were light and easy to handle by divers using SCUBA gear, and were held in place on the bottom at 12 m depth by rocks piled on the frame. *Pycnopodia helianthoides* and fresh dead market *Loligo opalescens* were placed in the containers and checked periodically.

Squid chosen for experiments were 30 - 33 cm in total length. Four squid pens removed from the above averaged 15.3 cm and were 2.1 cm at the widest point. The pen is flexible on the posterior end. A rib running the length of the pen is larger and adds strength to the pen at the anterior end. This semirigid anterior section, approximately 7 cm long, terminates in a sharp point.

RESULTS

Five subtidal tests (Table 1) were run in the isolation containers. Of 11 observed feedings, 10 squids were totally ingested by the sea stars within 10 minutes.

Of 26 sea stars tested in the isolation containers, 7 were found (26.9%) with a squid pen protruding through their aboral surface; the average protrusion was 2.9 cm. The average time of emergence of pens was 22.7 hrs, the range 19 - 27 hrs. The sea stars were not observed continually: the longest period between observations was 23 hrs; the average period was 7 hrs. The only timed observation outside the isolation containers was 19 hours, with the pen protruding 5 cm (Figure *2*).

Out of 9 sightings of pen protrusion (including 2 outside the isolation containers), 3 pens were measured to be 5 cm out through the aboral surface. All sequential observations of pen protrusion of a given sea star showed the pen to be protruding the same or an increased distance with time.

Close inspection of the aboral surface of sea stars in 4 trials showed the squid pen protruding through the papulae of the aboral disk (Figures *2, 3*). The position of the protruding squid pen of each of 6 observations is indicated diagrammatically in Figure 4. In no case was the pen protruding through the anus.

In all but one case of observed pen protrusion 2 to 4 rays were curled up around the pen. When rays were found in this position, another sea star touched to the test animal's opposite and normally positioned rays elicited movement and subsequent withdrawal of the curled rays. The protruding pen was then measured. These same test sea stars were re-inspected 3 or more hours later and all had replaced rays around the protruding pen.

DISCUSSION

Subtidal testing indicates that after *Pycnopodia helianthoides* feeds upon *Loligo opalescens* the indigestible squid pen is frequently extruded through the aboral surface of the sea star. While the pen has not actually been seen in a state of dropping out of the aboral surface, indications are that it does. Since the semi-rigid anterior section of the

Table 1

Summary of Results from Subtidal Isolation Containers
November 27, 1971 to March 21, 1972
Isolation container tests

Test	Number of *Pycnopodia* tested	Number with pens protruding	Distance of pen protrusion (cm)	Total time of test (hrs)
1	3	1	1.0	23.5
2	5	1	5.0	43.0
3	5	1	2.0	47.7
4	6	2	2.0 3.5	51.5
5	7	2	1.5 5.0	23.0
Total and Mean Values	26	7	2.8	37.7

Explanation of Figures *1* to *3*

Figure *1*: Subtidal isolation containers

Figure *2*: *Loligo opalescens* pen protruding approximately 5 cm from the aboral surface of *Pycnopodia helianthoides*

Figure *3*: Aboral surface of *Pycnopodia helianthoides* prior to squid pen protrusion. Note stretching of surface surrounding papulae

Figure *1*

Figure *2*

Figure *3*

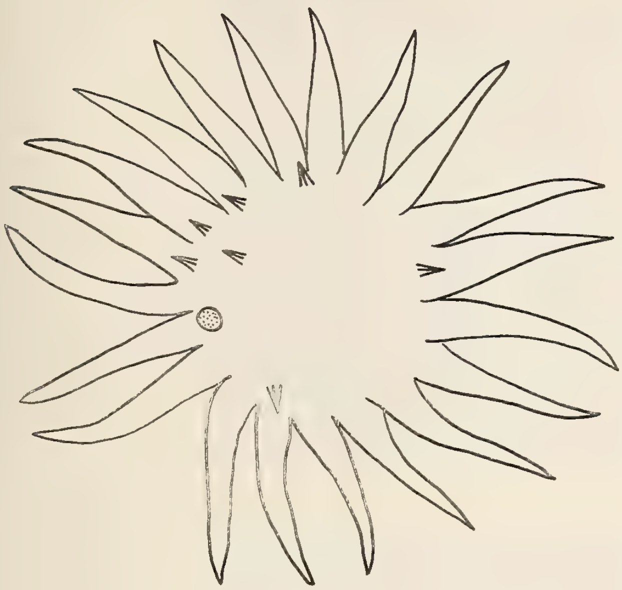

Figure 4

Aboral view of *Pycnopodia helianthoides* indicating approximate positions of seven *Loligo opalescens* pen protrusions. Composite drawing; dotted area represents the madreporite

pen, which emerges first, is about 7 cm long (in one trial a pen was found broken off into a section 5.5 cm long), it would seem reasonable that total elimination of at least some of the pens takes place in this manner. Also, since sequential observations of a given sea star reveal the pen to protrude the same or an increased distance out of the aboral surface, continued outward movement is indicated.

If one assumes the pen is pushed through the aboral surface for purposes of re-alignment, so it may be moved back through the cardiac stomach for oral elimination, it is difficult to understand why it would be pushed out as far as 5 cm which would leave approximately only 2 cm of semi-rigid pen within the sea star. The oral opening is large enough to eliminate more than a 2 cm object. Further, it seems that a pen already 5 cm out of the aboral surface and in a position to be grasped by tube feet, would more easily be pulled out completely than pushed (or pulled) back into the sea star for oral ejection.

A disturbed sea star which began lowering rays surrounding a protruding squid pen was seen to detach tube feet from the pen. The tube feet probably help eject the pen, at the same time cleaning it and removing food material that comes through the slit, a process which may serve the additional function of not attracting other predators to a possible food source. It would seem that less partly-digested squid material would be lost by aboral ejection than if the pen were forced out of the mouth. Also, the sea star can move and possibly continue to feed while the pen is partially protruding from its surface. It is possible that the position of the rays over the aboral surface represents a type of cleaning or feeding behavior of broader application, as on rare occasions sea stars are found in this position without a squid pen.

When the squid pen is forced through the aboral surface it comes out through the papulae, leaving a slit on the surface of the asteroid. If the pen cannot be eliminated in any other way than through the body wall, this is a logical site of elimination, as papulae are thin respiratory evaginations of the body wall that emerge between skeletal ossicles, and are known to be excretory in action (Hyman, 1955: 387; Ghiradella, 1965). Certainly forcing an object the size of a squid pen through a multitude of branched papulae is not the same as the tips of individual papulae constricting off waste products; however, if tips of papulae do constrict off, they are most likely capable of quickly healing, and rupture of this surface by the squid pen is probably not a traumatic physiological event to the sea star.

Note: While the above study was underway, 2 other examples of aboral extrusion of mollusk shells by sea stars were brought to my attention: a) Allyn G. Smith, California Academy of Sciences, San Francisco, California, reported that of 6 specimens of *Thrissacanthias penicillatus* Fischer, 1904, dredged in 180 to 360 m, due west of Pigeon Point, San Mateo County, California, 3 contained shells of *Solariella nuda* Dall, 1896. One of these sea stars had 2 shells within its stomach, one pushed partially through the aboral surface (Figures 5, 6). One shell was extracted through the mouth of a sea star for photographs and identification by Allyn Smith (Figure 7). The specimens were collected by Phillip Carlstroem, and are now in the California Academy of Sciences, Department of Invertebrate Zoology collection. b) Heidi Baird (Baird,

1972), a biology student, found a *Tegula* sp. shell had broken the aboral surface and was partially protruding from a live *Pycnopodia helianthoides* found in a tide pool off Pigeon Point, San Mateo County, California. The specimen was not preserved.

ACKNOWLEDGMENTS

I would like to thank biologist-divers Gary Carmignani, David L. Garrison, and Victor C. Norling for their able subtidal assistance; Drs. Robert D. Beeman and Jack T. Tomlinson, California State University San Francisco, for their advice and encouragement. Special thanks to Oceanic Products, San Leandro, California, for use of the research vessel *Octopus*, which served as a base of operations for many dives.

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Explanation of Figures *5* to *7*

Figure *5*: *Thrissacanthias pennicillatus* with shell of *Solariella nuda* partially through its aboral surface

Figure *6*: Close-up of aboral surface of *Thrissacanthias pennicillatus* with *Solariella nuda* shell protruding

Figure *7*: Shell of *Solariella nuda* after extraction from *Thrissacanthias pennicillatus*

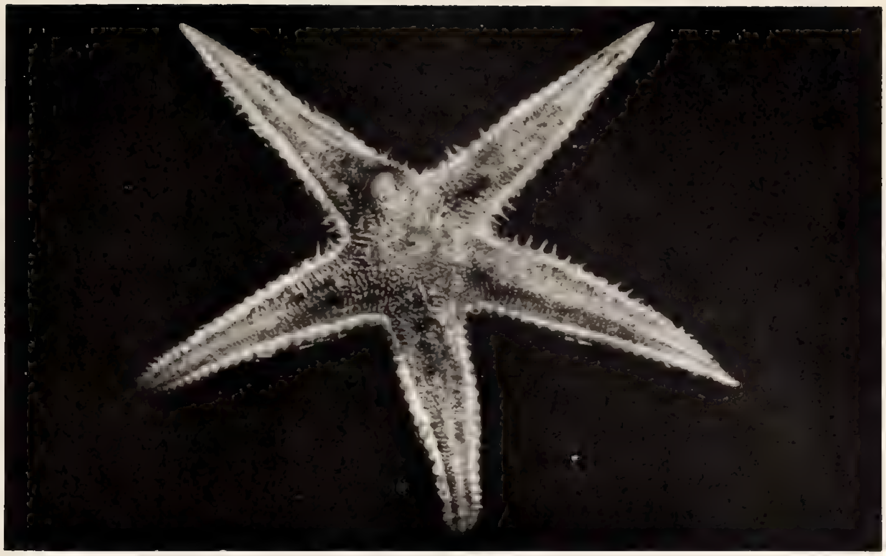

Figure 5

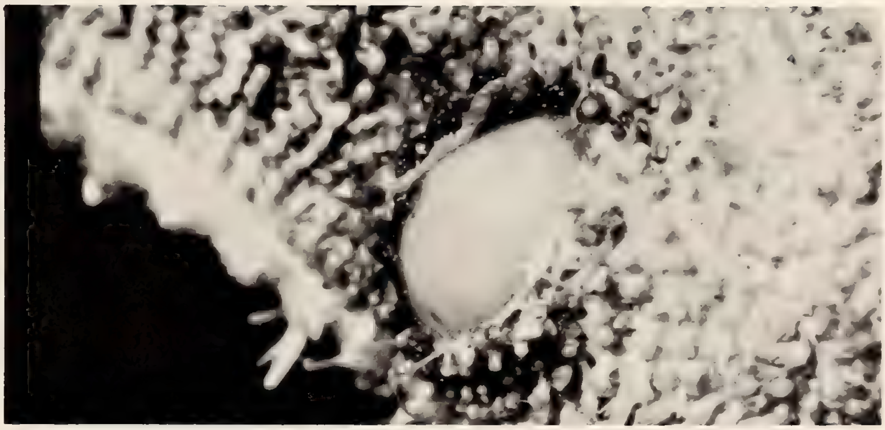

Figure 6

Figure 7

A Review of the Marginellidae Described by Bavay, 1903-1922

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(8 Text figures)

INTRODUCTION

Arthur Bavay (1840 - 1923) was a productive French malacologist who, between the years 1873 and 1923, published nearly 70 articles dealing with mollusks (Fischer, 1924), plus numerous short notices, and contributions to works of other authors. His scientific interests also included herpetology, parasitology, and medical natural history. In the course of his professional travels, which included sojourns in Guadeloupe and New Caledonia, he made many biological observations. Following his retirement from a distinguished career in pharmacy and health, in which he held national office, he devoted himself entirely to studies in malacology (Lamy, 1924). His areas of specialization included terrestrial and freshwater mollusks of the Far East, on which he collaborated with Philippe Dautzenberg; the migration of mollusks across the Suez Canal; the Pectinidae, of which he assembled a sizeable collection; and, among marine gastropods, the family Marginellidae.

In 15 publications, Bavay described a total of 39 new species and 18 infraspecific taxa in the Marginellidae. Reference citations for all of these publications appear in the bibliography of the present paper, including two works authored by Dautzenberg with descriptions of marginellid species contributed by Bavay. The species were, in general, quite adequately characterized in the original publications, and most were illustrated by excellent figures. Bavay was a skilled draftsman and scrupulous observer of detail in the minute shells which occupied much of his research, and he seems to have appreciated the value of good illustrations. Locality data were provided for almost all his described taxa, many of which came from French colonial possessions. Working as he did at the Muséum National d'Histoire Naturelle in Paris, Bavay had ready access to the type material of F. P. Jousseaume, another describer of many species of Marginellidae. Bavay (1922b) published some of Jousseaume's manuscript species after the latter's death.

Nevertheless, perhaps partly because they appeared too late for inclusion in the great 19th century monographs of the family, and partly because most of them were published in separate, short papers, Bavay's marginellid species have seldom been cited or recognized by subsequent authors. His latest works appeared after publication of Tomlin's (1917) comprehensive list of species of Marginellidae, and are therefore absent from that valuable compilation.

It is the purpose of this paper to bring all the Bavay marginellid species together in one reference, to suggest generic assignments based on modern concepts of marginellid classification, and to report on the status of relevant type material. In October 1971 the junior author had the opportunity to visit the mollusk collections of the Muséum National d'Histoire Naturelle to study and photograph the extant types. This study was aided by the generous assistance of Dr. Bernard Salvat of that institution. Those type specimens which could be located were in 3 areas of the museum: (1) the general collection (identified as "Coll. Gén." in the listing which follows), (2) a cabinet of types of species described in the Journal de Conchyliologie ("Coll. du Journal"), and (3) a drawer

labeled *Mission Gruvel,* containing in particular species collected by the Gruvel expeditions to West Africa in the early part of this century ("Mission Gruvel drawer"). A number of types could not be found, and in the absence of other evidence these are tentatively considered to be lost, on the advice of Dr. Salvat (letter to Roth, 12 May 1971). Missing, for example, are all but one type specimen of the species Bavay described in 1917; perhaps these were the victims of some mischance during World War I. Non-type material of some of the species is present in the general collection; and during Bavay's lifetime some material handled and identified by him was distributed to various other institutions. Authenticated specimens of this sort would be suitable candidates for neotype designations, should the need ever arise.

Fischer-Piette & Beigbeder (1944) published a list of marine gastropod types in the museum collection; and Fischer-Piette (1950) listed type material present in the Collection du Journal. These lists contain some but not all of Bavay's species. Where these reports differ from the junior author's findings, the fact is noted below.

A slightly different case of absent type material is that of Bavay's infraspecific taxa. It was Bavay's practice, as it was that of certain other malacologists of the time, to name "varieties" of his own and other authors' species. These were not conceived in the sense of geographic subspecies. For 17 of the 18 taxa he named in this form, Bavay did not segregate type material. From this fact, it is easy to infer that he himself did not consider his "varieties" to be of coordinate rank with his species. Investigation shows them, in most cases, to be nothing more than individual variants of their "parent" species; and in such instances we have not hesitated to relegate them to synonymy. It has sometimes been possible to recognize specimens with the characters of the varietal descriptions among non-type material of Bavay's in the museum collections.

For nomenclatural purposes, however, the varietal names cannot be dismissed so easily. According to Article 17 of the International Code of Zoological Nomenclature, "a name is or remains available even though ... before 1961, it was proposed as a 'variety' or 'form' ". In addition [Article 45(e)(i)], "before 1961, the use of either of the terms 'variety' or 'form' is not interpreted as an express statement of ... infrasubspecific rank." In other words, as long as they are accompanied by an indication, in the sense of Article 16 of the Code, and satisfy the other criteria of availability specified by Section IV of the Code, the names are available for application to their taxa, and must be recognized in questions of homonymy.

This interpretation was, in effect, applied by Tomlin (1917) when he considered the name *Marginella bivittata* Bavay in Dautzenberg, 1912, to be preoccupied by *Marginella chudeaui* var. *bivittata* Bavay in Dautzenberg, 1910, and renamed the former *Marginella ameliensis.* In this connection it is tempting to quote Tomlin (*op. cit.*: 242): "A point with regard to specific names which is much overlooked, especially by certain living authors who have a passion for varietal names, is that under the present code these [varietal] names are on precisely the same footing as the specific names in their genus. Consequently, and I may say fortunately, the inevitable multiplication of 'var. *major*', 'var. *minor*', 'var. *alba*', and the like has had the very opposite effect to that intended by their sponsors, and 99 per cent of them come into literature stillborn."

Of Bavay's 39 described nominal species, 31 are here treated as valid, 8 are considered junior subjective synonyms of other species. Of the 18 described "varieties" – 19 if Bavay's "var. B" of *Marginella hirasei* be counted – all but one are likewise synonymized. Further study may show that that one represents a valid geographic subspecies. An entry is also included for one unpublished name.

ACKNOWLEDGMENTS

The authors wish to express their gratitude for the many courtesies extended by Dr. Bernard Salvat, École Pratique des Hautes Études, Paris. Comparative work was made possible by the cooperation of personnel of the National Museum of Wales and the British Museum (Natural History). The kind assistance of S. Peter Dance, and the opinions and advice of Eugene V. Coan, A. Myra Keen, Nell H. Ludbrook and Peter U. Rodda are gratefully acknowledged.

EXPLANATION of FORMAT

Entries in the list which follows are arranged alphabetically by species name. Each entry contains: the specific or varietal name; authorship, if not simply attributed to Bavay; the genus of original proposal, if other than *Marginella*; date of publication; citation of original description and figure; type locality, bracketed information being supplied by the present authors; present status of type material and its location ("Coll. Gén.", "Coll. du Journal", or "Mission Gruvel drawer"); dimensions of type material; and modern generic allocation or synonymy. Where necessary, commentary follows each entry. Generic allocations are based partly on a classification of the family prepared by Eugene V. Coan and the senior author for the *Treatise on Invertebrate Paleontology.*

LIST OF MARGINELLIDAE DESCRIBED BY BAVAY

albida Bavay *in* Dautzenberg, *M. pallata* var. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 24. "Avec le type." No type material found. = *Gibberula pallata* (Bavay *in* Dautzenberg, 1912), *q. v.* (Not *Marginella triticea* var. *albida* Lamarck, 1822, nor *M. albida* Tate, 1878).

albina Bavay *in* Dautzenberg, *M. gruveli* var. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 25. Bay of Praia Amelia, 15 - 35 meters, and beach at Mossamedes [Angola]. No type material found. = *Persicula gruveli* (Bavay *in* Dautzenberg, 1912), *q. v.* (Not *Marginella albina* Gaskoin, 1853).

amazona Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 19 - 20; plt. 1, figs. 19, 20. Cotonou [Dahomey]. Holotype, Mission Gruvel drawer, MNHNP. 20.4 × 12 mm. *Marginella (Marginella).*

On shell characters this species appears to stand near *Marginella helmatina* Rang, 1832, and *M. cumingiana* Petit, 1841. It differs from the other two species mainly in having many wavy longitudinal color lines, a more flared outer lip, and in the development of a heavy pad of callus across the parietal wall. In *M. helmatina* and *M. cumingiana* the axial lines disappear after 3 or 4 turns of growth. It may be correct to regard this as a southern subspecies of *M. helmatina*. It is evidently rare. Referable museum specimens include one 24 mm long in the British Museum (Natural History) (Reg. No. 1936.4.17.50), and a 25 mm specimen in the Muséum d'Histoire Naturelle in Geneva.

ambigua Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 22 - 23; plt. 1, figs. 21, 22. Rio de Oro [Spanish Sahara]. Holotype, Mission Gruvel drawer, MNHNP. 14.0 × 6.0 mm. = *Volvarina deliciosa* (Bavay *in* Dautzenberg, 1912).

The subjective characters by which Bavay distinguished *Marginella ambigua* from his *M. deliciosa* are imprecise, and the features of the holotype of *M. ambigua* can be duplicated in a lot of about 30 topotypic *M. deliciosa* in the general collection. Since both names date from the same publication, in synonymizing them we are acting as "first revisers" in the sense of Article 24 (a) of the International Code of Zoological Nomenclature.

Bavay had two specimens of *Marginella ambigua*. One was the present holotype; the other, a bandless individual, was designated as the "var. *concolor*" (*in* Dautzenberg, 1912: 22). This specimen was not found by the junior author; it is certain to be another synonym of *Volvarina deliciosa*.

atomella, Marginella (Granula). Aug. 1917. Journ. de Conchyl. 63 (2): 101 - 102; plt. 2, fig. 6. Mauritius and Réunion. Type not found. Given as 0.8 × 0.6 mm. = *Granulina pulvis* (Jousseaume, 1875).

The type was not present in the Journal Collection in 1950 (Fischer-Piette, 1950) and could not be located by the junior author. Bavay (1922a: 57 - 59) later synonymized this species with *Granulina pulvis* (Jousseaume, 1875), and, considering that Réunion is the type locality of the latter species, this seems entirely plausible.

aurata Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 26; plt. 1, figs. 33, 34. Bay of Mossamedes [Angola], 15 - 20 meters. Holotype, Mission Gruvel drawer, MNHNP. 2.5 × 1.5 mm. *Gibberula.*

The unique holotype has an indented canal in the anterior margin, which does not show well in the original illustration.

bivittata Bavay *in* Dautzenberg, *M. chudeaui* var. 1910. Actes Soc. Linn. Bordeaux 64: 89. Port Etienne, Cansado Bay, etc. No type material found. = *Gibberula chudeaui* (Bavay *in* Dautzenberg, 1910), *q. v.*

bivittata Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 23; plt. 1, figs. 23, 24. Bay of Praia Amelia, 15 - 35 meters. Holotype, Mission Gruvel drawer, MNHNP. 8.0 × 4.0 mm. = *Volvarina ameliensis* (Tomlin, 1917). (Not *Marginella chudeaui* var. *bivittata* Bavay *in* Dautzenberg, 1910).

Tomlin (1917: 252, 254) renamed this species on account of the prior *Marginella chudeaui* var. *bivittata*. Its relationship to *Volvarina exilis* (Gmelin, 1791) seems close.

bougei. Aug. 1917. Journ. de Conchyl. 63 (2): 103 - 104; 67 (1): plt. 1, figs. 6, 7. Ouvea, Wallis Islands. Holotype, Coll. du Journal, MNHNP. 1.4 × 0.7 mm. *Granulina.*

By error, the figure accompanying the original description (1917: plt. 2, fig. 3) showed another species. The holotype was later correctly figured by Bavay (1922a), at which time he reported the species from New Caledonia.

cherubini. Nov. 1922. Journ. de Conchyl. 67 (1): 64 - 65; plt. 1, fig. 8. Seychelles Islands. Holotype, Coll. du Journal, MNHNP. 3.5 × 2.5 mm. *Persicula.*

Dautzenberg (1929) reported this species from Madagascar, based on identifications by Bavay.

chudeaui Bavay *in* Dautzenberg. 1910. Actes Soc. Linn. Bordeaux 64: 87 - 88; plt. 2, figs. 1, 2. Dredged, Cansado Bay [Mauritania; label with type]. Holotype, Mission Gruvel drawer, MNHNP. Length 4.5 mm. *Gibberula*.

Descriptions of Bavay's "varieties", *major, elongata, quinquevittata, trivittata, bivittata,* and *univittata* (*in* DAUTZENBERG, 1910: 88 - 89), for which no type material was found to be segregated, suggest only individual variants of the species. Specific localities for the varieties were not published.

clandestinella, M. clandestina Brocchi, var. March 1908. Journ. de Conchyl. 55 (4): 344. Martinique. No type material found. Size "one-third smaller than *M. clandestina.*" See next entry.

clandestinella. 1913. Bull. Mus. Nat. Hist. Nat. 19 (6): 358 - 359; text figs. 1, 2. Bahia, Brazil. Four syntypes, marked "cotypes", Coll. Gén. Length 1.5 mm. = *Granulina ovuliformis* (Orbigny, 1841).

If "*Marginella clandestina* Brocchi, var. *clandestinella*", with its very brief description, be considered a *nomen nudum,* then *Marginella clandestinella* of 1913 is validly proposed; otherwise, being published in synonymy of the former, the latter name is technically unavailable. As the specific epithet is the same in both cases, the question is principally of theoretical interest. The 4 "cotypes" from Bahia are all that we have to demonstrate Bavay's concept of both taxa, so regardless of the nomenclatural solution they may be considered to have the weight of primary type material.

The authors are unable to suggest any characters of the "cotypes" which would differentiate them from *Granulina ovuliformis* (Orbigny). The latter is the oldest of several names applied to Caribbean members of the genus; the actual number of species in the province awaits determination.

columnella Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 26; plt. 1, figs. 31, 32. Bay of Praia Amelia, 15 - 35 meters. Holotype, Mission Gruvel drawer, MNHNP, 2.8 × 1.5 mm. *Granula*.

concolor Bavay *in* Dautzenberg, *M. ambigua* var. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 22. Rio de Oro [Spanish Sahara]. No type material found. = *Volvarina deliciosa* (Bavay *in* Dautzenberg, 1912). See discussion under *M. ambigua* above.

concolor Bavay *in* Dautzenberg, *M. gruveli* var. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 25. "Avec le type à Praya-Amelia." No type material found. = *Persicula gruveli* (Bavay *in* Dautzenberg, 1912). *q. v.*

corallina, Marginella (Volvarina). June 1910. Journ. de Conchyl. 58 (1): 22 - 23; plt. 1, figs. 1, 2. Cape Verde Islands. Holotype, in Coll. du Journal, *fide* FISCHER-PIETTE (1950), but not found by present authors. Given as 5 × 1.6 mm. *Volvarina*.

The description and figures strongly suggest *Volvarina mediocincta* (E. A. Smith, 1875), also from the Cape Verdes, and the two may be synonymous.

decaryi, Marginella (Volvaria). Nov. 1920. Journ. de Conchyl. 65 (2): 164 - 165; 2 text figs. Between False Cape and Cape Sainte-Marie, Madagascar. Holotype, Coll. Gén., MNHNP. 2.4 × 0.8 mm. *Ovaginella*.

The holotype resembles *Marginella cylichnella* May, 1917, which was placed in *Ovaginella* by LASERON, 1957.

deliciosa Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 21 - 22; plt. 1, figs. 25, 26. 3.5 miles north of Point Cansado [Mauritania], 9 - 10 meters. Holotype, Mission Gruvel drawer, MNHNP. 12.0 × 6.0 mm. *Volvarina*.

The holotype was evidently selected from a lot of about 30 specimens now in the general collection which vary in color from white to pinkish, with some specimens having 2 pairs of darker, spiral, parallel bands on the body whorl. Bavay's "var. *efasciata*" (*in* DAUTZENBERG, 1912: 22), which was said to be found with the typical species and for which no type was segregated, is clearly only the pale, unbanded color form.

delphinica. Nov. 1920. Journ. de Conchyl. 65 (2): 165 to 166; 2 text figs. Between False Cape and Cape Sainte-Marie, Madagascar. Holotype, Coll. Gén., MNHNP. 3.0 × 1.5 mm. ?*Alaginella*.

None of the species originally placed by LASERON (1957) in *Alaginella* have axial plications, but. *M. delphinica* appears similar in other respects. *Plicaginella* (type species, *Marginella formicula* Lamarck, 1822) is plicate, but has a deep anterior notch.

dispoliata (Jousseaume MS). 1922. Bull. Mus. Nat. Hist. Nat. 28 (1): 76 - 77; text fig. 1. Djibouti [French Somaliland], subfossil. Type not found. Given as 3 × 1.5 mm. *Dentimargo*. (Figure 1).

efasciata Bavay *in* Dautzenberg, *M. deliciosa* var. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 22. "Habite avec le type." No type material found. = *Volvarina deliciosa* (Bavay *in* Dautzenberg, 1912), *q. v.* (Not *Marginella miliaria* var. *efasciata* Monterosato, 1875, a *nomen nudum, fide* TOMLIN, 1917).

Figure 1

Marginella dispoliata Bavay, *ex* Jousseaume MS.
Copy of original figure

elongata Bavay *in* Dautzenberg, *M. chudeaui* var. 1910. Actes Soc. Linn. Bordeaux 64: 88. Port Etienne, Cansado Bay, etc. No type material found. = *Gibberula chudeaui* (Bavay *in* Dautzenberg, 1910), *q. v.*

fischeri. Mar. 1903. Journ. de Conchyl. 50 (4): 407 - 408; plt. 8, figs. 10, 11. Locality unknown. Holotype, Coll. du Journal, MNHNP. 10.5 × 6.5 mm. *Cryptospira.*

Specimens agreeing well with the holotype of this species have recently been dredged in 64 m off southern Palawan, Philippine Islands (material in junior author's private collection). Some have 1, 2, or 4 narrow reddish spiral bands, instead of the 3 exhibited by the type; the 4-banded condition is most common.

Bavay compared *Marginella fischeri* to *M. tricincta* Hinds, 1844, type species of the genus *Cryptospira*. In having the spire visible instead of immersed, however, it is more similar to the holotype of *M. immersa* Reeve, 1865, in the British Museum (Natural History). The latter shell is beachworn and white.

fulva, Marginella (Volvaria) serrei var. 1913. Bull. Mus. Nat. Hist. Nat. 19 (7): 483. Bahia, Brazil. No type material found. = *Volvarina serrei* (Bavay, 1913), *q. v.*

gemmula Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 20 - 21; plt. 1, figs. 17, 18. [Bay of Praia Amelia, 15 - 35 meters; label with type.] Holotype, Mission Gruvel drawer, MNHNP. 5.0 × 3.0 mm. *Marginella (Simplicoglabella).*

germaini, Marginella (Volvaria). 1913. Bull. Mus. Nat. Hist. Nat. 19 (7): 483; plt. 20, figs. 1, 2. Bahia, Brazil. Type not found. Given as 3.5 × 1.8 mm. *Volvarina.*

goubini. Nov. 1922. Journ. de Conchyl. 67 (1): 60 - 61; plt. 1, fig. 10. Lifou [Loyalty Islands]. Holotype lost from Coll. du Journal. Given as 2.7 × 1.25 mm. *Euliginella.*

The unique holotype was present in the Journal Collection in 1950 (Fischer-Piette, 1950), but a note on its box indicates that it has been missing since 1964.

gruveli Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 24 - 26; plt. 1, figs. 29, 30. Bay of Mossamedes, 15 - 20 meters [label with type]. Holotype, Mission Gruvel drawer, MNHNP. 6.5 × 4.0 mm. *Persicula.*

No type material was found segregated for Bavay's "var. *concolor*" and "var. *albina*" (*in* Dautzenberg, 1912: 25). Some lots of *M. gruveli* in the general collection, from the other localities mentioned in the original publication, may contain the specimens upon which Bavay based his varieties. The epithet "*albina*" is preoccupied in *Marginella,* and Bavay also applied the name "*concolor*" to a variety of *Marginella ambigua* in the same paper.

hervieri. Nov. 1922. Journ. de Conchyl. 67 (1): 61 - 62; plt. 1, figs. 1, 2. Lifou [Loyalty Islands]. Holotype, Coll. du Journal, MNHNP. 3.4 × 2.0 mm ?*Eratoidea.*

hirasei, Marginella (Volvaria). Aug. 1917. Journ. de Conchyl. 63 (2): 106 - 108; plt. 2, fig. 9. Kikai [Amami Islands]. Type not found. Given as 7 × 2 mm. *Volvarina.*

The holotype was not present in the Journal Collection in 1950 (Fischer-Piette, 1950) and could not be located by the junior author. Also absent was material of Bavay's "var. B" (1917: 107), which from its description appears to be an unbanded individual of the same species.

joubini, Marginella (Volvaria). 1913. Bull. Mus. Nat. Hist. Nat. 19 (7): 483; plt. 20, figs. 3, 4. Bahia, Brazil. Holotype, with label by Fischer, 1942, Coll. Gén., MNHNP. Length 4.5 mm. = *Volvarina bahiensis* (Tomlin, 1917) (Not *Marginella (Volvarina) joubini* Dautzenberg & H. Fischer, 1906.)

The outer lip of the holotype has been broken back about to the growth line visible in the original figure. It is a juvenile shell. Its evident slimness suggests close relationship if not identity with *Volvarina gracilis* (C. B. Adams, 1850); both species were reported from Brazilian localities by Rios (1970).

It was renamed *Marginella bahiensis* by Tomlin (1917: 252, 273).

jullieni, M. miliaris [*sic*] L., var. Aug. 1917. Journ. de Conchyl. 63 (2): 96 - 97; plt. 2, fig. 1. Grand-Cess, Garraway, Liberia. Type not found. Given as 3 × 2 mm. ? = *Gibberula miliaria* (Linnaeus, 1758).

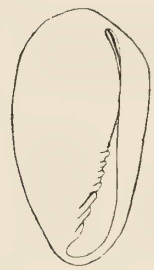

Figure 2
Marginella (Volvaria) larva Bavay
Copy of original figure

larva, Marginella (Volvaria). 1922. Bull. Mus. Nat. Hist. Nat. **28** (6): 427 - 428; text fig. 4. Colon [Canal Zone]. Nine syntypes, marked "cotypes", Coll. Gén., MNHNP. Length 2 - 4 mm. *Cystiscus.* (Figure 2.)

Cystiscus larva is an earlier name for *Gibberula bocasensis* Olsson & McGinty (1958: 39; plt. 4, fig. 10), which was originally cited as occurring at Colon. The latter species was first placed in *Cystiscus* by Keen (1971), in comparison with the similar west American *C. politulus* (Dall, 1919).

louisae. 1913. Bull. Mus. Nat. Hist. Nat. **19** (5): 297; text fig. Réunion. Four syntypes, Coll. Gén., MNH NP, with label by Fischer, 1943. Length 2 - 2.25 mm. *Granula.*

Figure 3
Marginella (Glabella) macnairi Bavay
Copy of original figure

macnairi, Marginella (Glabella). 1922. Bull. Mus. Nat. Hist Nat. **28** (6): 426; text fig. 2. Colon [Canal Zone; label with types]. Fourteen syntypes, Coll. Gén., MNHNP. Length 2 - 2.5 mm. = *Dentimargo aureocincta* (Stearns, 1873). (Figure 3.)

Dentimargo aureocincta was reported from the Caribbean coast of Panama by Olsson & McGinty (1958).

major Bavay *in* Dautzenberg, *M. chudeaui* var. 1910. Actes Soc. Linn. Bordeaux **64**: 88. Port Etienne, Cansado Bay, etc. No type material found. = *Gibberula chudeaui* (Bavay *in* Dautzenberg, 1910), *q. v.*

The several prior applications of the epithet "*major*" in Marginellidae, as compiled by Tomlin (1917), appear to be *nomina nuda.*

micros, Marginella (Volvaria). Nov. 1922. Journ. de Conchyl. 67 (1): 63 - 64; plt. 1, figs. 3. Tuamotu Islands. Holotype, Coll. du Journal, MNHNP. 1.5 × 0.8 mm. ?*Cystiscus.*

The holotype agrees in most respects with the description of *Halоginella infans* Laseron (1957: 299 - 300; fig. 66) from Mast Head Island, Capricorn Group, Queensland.

minor, M. pulchella Kiener, var. Nov. 1920. Journ. de Conchyl. 65 (2): 163. Madagascar. No type material found. = *Persicula pulchella* (Kiener, 1834).

Preoccupied by *Marginella minor* C. B. Adams, 1852.

montrouzieri. Nov. 1922. Journ. de Conchyl. 67 (1): 62 to 63; plt. 1, figs. 4, 5. Lifou [Loyalty Islands]. Holotype Coll. du Journal, MNHNP. 1.5 × 1.0 mm. *Crithe.*

The holotype is a juvenile shell, with thin outer lip. In the course of describing *M. montrouzieri,* Bavay introduced 2 *nomina nuda*: "*M. wardeni* Iredale" and "*M. wallacei* Iredale" (not *Egouena wallacei* Jousseaume, 1875). Museum lots labeled with the Iredale manuscript names, from the Kermadec Islands, exist in the British Museum (Natural History) (Reg. Nos. 1911.11.2.117 to 119, and 1911.11.2.120 to 122), and possibly elsewhere; these specimens closely resemble the holotype of *Granulina bougei* (Bavay, 1917).

(*morgani* Bavay MS. Two specimens, Coll. Gén., MNH NP, from Perim Island, southern Red Sea, bear this unpublished name. They are undoubtedly specimens of a described species of *Granulina.*)

pallata Bavay *in* Dautzenberg. Dec. 1912. Ann. Inst. Océanogr. 5 (3): 24; plt. 1, figs. 27, 28. Bay of Praia Amelia, 15 - 35 meters [label with type]. Holotype, Mission Gruvel drawer, MNHNP. 5.5 × 3.5 mm. *Gibberula.*

Bavay's "var. *pallida*" and "var. *albida*" (*in* Dautzenberg, 1912: 24), for which no type material was segre-

gated, are merely color forms of this species. Both of the varietal names have prior usage in Marginellidae.

pallida Bavay *in* Dautzenberg, *M. pallata* var. Dec. 1912. Ann. Inst. Océanogr. 5 (3) : 24. "Avec le type." No type material found. = *Gibberula pallata* (Bavay *in* Dautzenberg, 1912), *q. v.* (Not *Bulla pallida* Linnaeus, 1758; *Volvaria pallida* Blainville, 1829; *Marginella miliaria* var. *pallida* Bucquoy, Dautzenberg & Dollfus, 1883; etc. See Tomlin, 1917.)

perexilis. 1922. Bull. Mus. Nat. Hist. Nat. 28 (1) : 78 - 79; text fig. 3. Paraíba, Brazil. Type not found. Given as 3.4 × 1.3 mm. *Dentimargo.* (Figure 4.)

Bavay compared the species to his *M. joubini,* but the illustration looks like a species of *Dentimargo,* possibly *D. aureocincta* (Stearns, 1873).

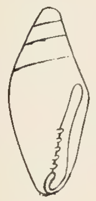

Figure 4

Marginella perexilis Bavay
Copy of original figure

perrieri, Marginella (Volvarina) [*Marginella (Volvaria)* on plate]. Feb. 1906. Journ. de Conchyl. 53 (3) : 248 to 249; plt. 7, figs. 5, 6. Malouines Insulas [Falkland]. Type not found. Given as 11 × 5 mm. *Volvarina.*

Bavay's original figure shows a small hole just below the spire which should make the figured specimen easy to identify if ever found. This species was reported from the Rio Plata area of Uruguay and Argentina by Carcelles (1953). As remarked by Bavay, its relationship to *Volvarina avena* (Kiener, 1834) of Brazil and the Caribbean seems close.

pupa. 1922. Bull. Mus. Nat. Hist. Nat. 28 (1) : 79 - 80; text fig. 4. Paraíba, Brazil. Type not found. Given as 3.6 × 1.4 mm. *Volvarina.* (Figure 5.)

The figure looks like a juvenile shell, although some thickening of the outer lip is mentioned. Bavay suggested assignment to *Volvarina.*

Figure 5

Marginella pupa Bavay
Copy of original figure

quinquevittata Bavay *in* Dautzenberg, *M. chudeaui* var. 1910. Actes Soc. Linn. Bordeaux 64: 89. Port Etienne, Cansado Bay, etc. No type material found. = *Gibberula chudeaui* (Bavay *in* Dautzenberg, 1910). *q. v.*

reducta, Marginella (Glabella). 1922. Bull. Mus. Nat. Hist. Nat. 28 (6) : 426 - 427; text fig. 3. Cuba. Type not found. Given as 3 × 1.6 mm. *Dentimargo.* (Figure 6.)

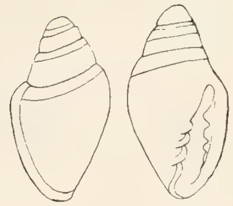

Figure 6

Marginella (Glabella) reducta Bavay
Copy of original figure

roberti (de Monterosato MS), *Marginella (Volvaria).* Aug. 1917. Journ. de Conchyl. 63 (2) : 104 - 106; plt. 2, fig. 8. Madeira Islands. Type not found. Given as 9 × 4 mm. ?= *Volvarina mitrella* (Risso, 1826).

rosea, M. lantzii Jousseaume, var. Nov. 1920. Journ. de Conchyl. 65 (2) : 163 - 164. Madagascar. No type material found. = *Dentimargo lantzii* (Jousseaume, 1875), ? subsp.

Preoccupied by *Marginella rosea* Lamarck, 1822.

rosea, M. pumila Redfield, var. Nov. 1920. Journ. de Conchyl. **65** (2): 164. Madagascar. No type material found. = *Eratoidea pumila* (Redfield, 1870).

Preoccupied by *Marginella rosea* Lamarck, 1822. Dautzenberg (1929) reported both typical *M. pumila* and this variety from southern Madagascar localities.

serrei, Marginella (Volvaria). 1913. Bull. Mus. Nat. Hist. Nat. **19** (6): 359 - 360; fig. 3. Bahia, Brazil. Four syntypes, marked "cotypes", and a lot of 13 paratypes, Coll. Gén., MNHNP; two paratypes, National Museum of Wales. Length 5 - 6 mm. *Volvarina.*

Fischer-Piette & Beigbeder (1944) reported 5 syntypes present. Bavay's "var. *fulva*" (1913c: 483), for which no type material was segregated, is probably only a color form; it was synonymized with the species by Rios (1970).

Ludbrook (1958) mentioned this species in describing *Volvarina* (?) *incommoda*; that species, however, belongs in *Canalispira* Jousseaume, 1875, and represents the first recorded Pliocene occurrence of that genus.

serrei, Marginellopsis. 1911. Bull. Mus. Nat. Hist. Nat. **17** (4): 240 - 243; text fig. 1. Cuba. Eight probable syntypes labeled "Serre, M. P. in 1911 (8) Cuba", Coll. Gén., MNHNP. Length 1 mm. Type species, by monotypy, of *Marginellopsis* Bavay, 1911.

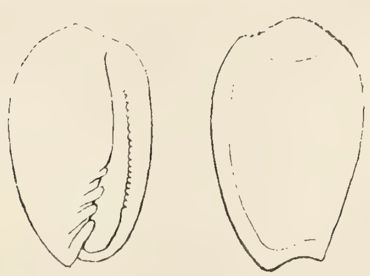

Figure 7

Marginella terverianella Bavay, *ex* Jousseaume MS.
Copy of original figure

terverianella (Jousseaume MS). 1922. Bull. Mus. Nat. Hist. Nat. **28** (1): 80 - 81; text figs. 5, 5a. Djibouti [French Somaliland]. Type not found. Given as 4 × 2.6 mm. ?*Gibberula.* (Figure 7.)

tomlini. Aug. 1917. Journ. de Conchyl. **63** (2): 102 - 103; plt. 2, fig. 7. Ouvea, Wallis Islands. Type not found. Given as 2.5 × 1.15 mm. *Cystiscus.* (Not *Marginella tomlini* Shackleford, 1916).

The type specimen was not present in the Journal Collection in 1950 (Fischer-Piette, 1950) and could not be located by the junior author. The name is a primary homonym of *Marginella tomlini* Shackleford 1916; the present state of our knowledge of minute Indo-Pacific Marginellidae makes its renaming inadvisable at this time.

trivittata Bavay *in* Dautzenberg, *M. chudeaui* var. 1910. Actes Soc. Linn. Bordeaux **64**: 89. Port Etienne, Cansado Bay, etc. No type material found. = *Gibberula chudeaui* (Bavay *in* Dautzenberg, 1910), *q. v.*

turbiniformis. Aug. 1917. Journ. de Conchyl. **63** (2): 98 - 99; plt. 2, fig. 2. Lifou [Loyalty Islands]. Type not found. Given as 3 × 2 mm. *Protoginella.*

The type material was absent from the Journal Collection in 1950 (Fischer-Piette, 1950). The general collection contains one lot of 6 shells, 2.5 to 3 mm long, which resemble the original illustration, but no single specimen could be matched to the figure.

univittata Bavay *in* Dautzenberg, *M. chudeaui* var. 1910. Actes Soc. Linn. Bordeaux **64**: 89. Port Etienne, Cansado Bay, etc. No type material found. = *Gibberula chudeaui* (Bavay *in* Dautzenberg, 1910), *q. v.*

(var. B, *Marginella (Volvaria) hirasei.* Aug. 1917. Journ. de Conchyl. **63** (2): 107. Oshima [Amami Islands]. No type material found. = *Volvarina hirasei* (Bavay, 1917), *q. v.*

Figure 8

Marginella virgula Bavay, *ex* Jousseaume MS.
Copy of original figure

virgula (Jousseaume MS). 1922. Bull. Mus. Nat. Hist. Nat. **28** (1): 78; text fig. 2. Perim [Island, southern Red Sea; label with type lot]. Lot of about 56 probable syntypes, Coll. Gén., MNHNP, with label by Fischer, 1942. Given as 3.8 × 2 mm. = *Granula louisae* (Bavay, 1913). (Figure 8.)

The original figure does does not show that the anterior margin is indented into a shallow notch, as in the prob-

able syntypes. DAUTZENBERG (1929) reported this species from Madagascar, based on determinations by Bavay. It appears to be a synonym of *Granula louisae* (Bavay, 1913), described from Réunion.

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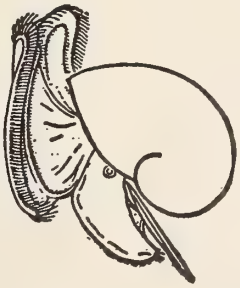

A New Species of Anaspidean Opisthobranch from the Gulf of California

(Mollusca : Gastropoda)

BY

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(1 Map; 15 Text figures)

INTRODUCTION

THE GULF OF CALIFORNIA abounds in its variety and number of species of opisthobranch gastropods. These include a fair mixture of Californian, Panamic, Indo-Pacific, and circumtropical species. The order Anaspidea is quite well represented in the fauna of the Gulf. Eight species of anaspideans have been reported from these waters. Of these, *Dolabrifera dolabrifera* (Rang, 1828), *Stylocheilus longicauda* (Quoy & Gaimard, 1824), *Aplysia parvula* Mörch, 1863, and *Aplysia juliana* Quoy & Gaimard, 1832, are of circumtropical distribution. KEEN (1971: 810) states that *Dolabella auricularia* (Lightfoot, 1786) is widely distributed in the Indo-Pacific. *Dolabella californica* Stearns, 1877 is known only from the Gulf. MARCUS & MARCUS (1970: 191) consider the *Dolabella californica* of MACFARLAND (1966) to be synonymous with *D. auricularia*. A formal synonymy of the 2 species is not given, however, and therefore 2 distinct species will be recognized here. The remaining 2 species, *Aplysia californica* Cooper, 1863 and *A. vaccaria* Winkler, 1955 are known from the coast of California as well as from the Gulf.

On December 23, 1970, some algal material (*Padina* sp.) was collected near San Carlos, Sonora, Mexico, to be used as a background for photographing several opisthobranchs collected the previous day. It was noted, however, that another opisthobranch was crawling actively along the algal surface. Direct observation of more of the same algae yielded several additional individuals of this dolabriferid anaspidean. Subsequent investigation of the material showed this animal to belong to an undescribed species, readily assignable to the genus *Phyllaplysia*.

Additional observations and specimens were obtained on a trip to Puertecitos, Baja California, in the spring of 1972. Two animals of the same species were collected on March 28, 1972 from the intertidal volcanic shores near Puertecitos.

Phyllaplysia padinae Williams & Gosliner, spec. nov.

Diagnosis: Penis armed; penial spines mammiform; penis tip cleft dorsally. Male aperture located antero-ventrally to right eye. Hermaphroditic gonopore located near anterior region of dorsal slit. Gonad narrow, elongate. Duct of bursa copulatrix arising from common atrium. Radular formula approximately $18 \times 8\text{-}21 \cdot 1 \cdot 1 \cdot 1 \cdot 8\text{-}21$. Rachidian teeth tricuspid, cusps acute; first pleural teeth tall, with 3 obtuse cusps; other lateral teeth short, with broad, flattened edge and 2 adjacent, smaller cusps; labial plates armed; labial armature tall, mammillate; jaws armed; masticatory armature of dense, tall, hook-tipped rodlets; gizzard teeth cornucopiate, uniform in structure. Shell a flat plate with central calcified portion and transparent margin; shell composed of concentric rings surrounding central apex. Cerebral commissure length approximately equal to cerebral ganglion diameter. Body color uniform olive green with scattered white spots; body often with minute papillae; papillae, when present, highly variable in shape and number. Body length not exceeding 45 mm; body slender, visceral hump reduced. Rhinophores short, bulbous, slit from distal ends ½ their length. Cephalic tentacles slit entire length to base; cephalic tentacles commonly held at right angles to each other in actively crawling animals. Oral tentacles elongate triangular, acute at tips. Foot broadest just posterior to middle of body in actively crawling animals; foot margin and edge of dorsum joined throughout.

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Type Material: The holotype of ***Phyllaplysia padinae*** is deposited in the Invertebrate Zoology Type Collection of the California Academy of Sciences, San Francisco, California, where it bears the number CASIZ 591; also deposited are the shell (CASIZ 592) and radula (CASIZ 593) of paratype specimens. Other paratype material remains in the private collections of the authors.

Name: The specific name ***padinae*** is derived from the name of the dictyotalean phaeophyte alga *Padina durvillaei* Bory de Saint Vincent, 1827 on which the animal is most often encountered.

Taxonomic Position in the subclass Opisthobranchia:

APLYSIIDAE

Dolabriferinae

Phyllaplysia P. Fischer, 1872

Phyllaplysia padinae

WORLD SPECIES LIST

The following is a list of species names presently in use in the genus *Phyllaplysia*.

1. *Phyllaplysia brongniartii* (Blainville, 1825)
2. *P. depressa* (Cantraine, 1835)
3. *P. engeli* Marcus, 1955
4. *P. inornata* Bergh, 1905
5. *P. lafonti* (P. Fischer, 1870)
6. *P. ornata* (Deshayes, 1853)
7. *P. padinae* Williams & Gosliner, 1973
8. *P. paulini* Mazzarelli, 1895
9. *P. plana* Eales, 1944
10. *P. taylori* Dall, 1900
11. *P. varicolor* (Bergh, 1905)
12. *P. viridis* (Bergh, 1905)

Type Locality: The type locality of ***Phyllaplysia padinae*** is the San Carlos Bay region directly northwest of Guaymas, Sonora, Mexico. Individuals were encountered only on the outer coast of the point forming the southern portion of San Carlos Bay (27°55′N lat.; 111°05′W long.).

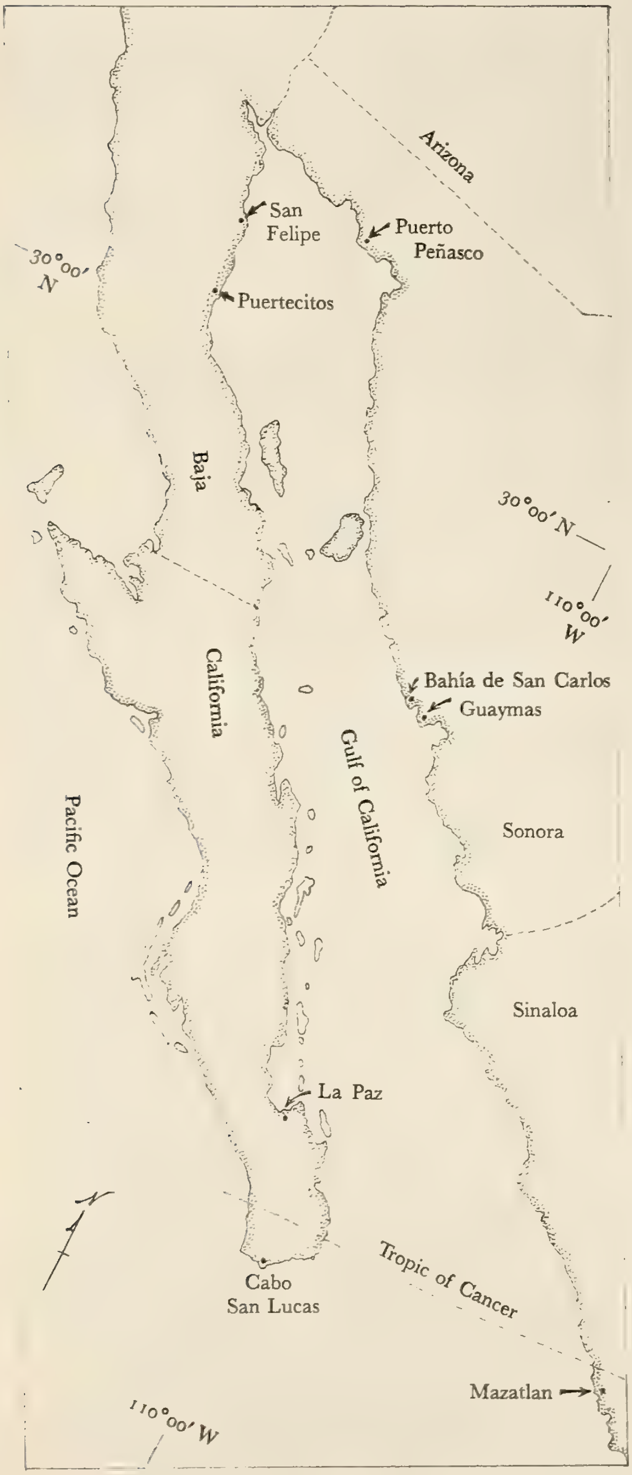
NATURAL HISTORY

Some of the qualitative aspects of the biodynamics of San Carlos Bay have been discussed by GOSLINER & WILLIAMS (1972: 425 and 432). Though San Carlos Bay represents a unique heterogeneous ecosystem, the reef region where ***Phyllaplysia padinae*** was originally collected represents a more typical intertidal to subtidal region similar to the major part of the coastline of the Gulf of California. The region consists largely of lava reefs which drop off deeply just beyond the extreme low tide zone. On one side of the reef the water remains shallow and the depth increases gradually. Here the substrate consists largely of coarse sand. While this particular reef region is subject to many of the same abiotic variables, a wide range of habitat diversity exists.

Distribution: Additional individuals (not type material) have been collected from 2 other localities. Mr. Wesley Farmer (personal communication) has taken ***Phyllaplysia padinae*** from Puerto Peñasco, Sonora (31°20′N lat.; 113°38′W long.). The open reef habitat at Puerto Peñasco is ecologically quite similar to that at the San Carlos reef. We collected 2 large individuals of ***P. padinae*** from tide pools on a large lava rock outcrop 2.4km north of Puertecitos, Baja California (30°25′N lat.; 114°40′W long.). This rocky area is different in that it is completely surrounded by sand flats. Despite this great ecological difference from the 2 other localities, the marine life supported by this volcanic outcrop is very similar in species make-up and in relative numbers. The present geographic range of ***Phyllaplysia padinae*** is from Bahía de San Carlos, Sonora to Puerto Peñasco, Sonora and Puertecitos, Baja California. It would appear, therefore, that the range probably extends throughout the northern portion of the Gulf of California (see Map).

Habitat: At the type locality (Bahía de San Carlos) ***Phyllaplysia padinae*** occurs in at least 2 distinct habitats. The first occurs immediately below the extreme high tidal region largely inhabitated by the isopod *Ligia occidentalis* Dana, 1853 and various crabs. This area is characterized by very small pools at low tide dominated by the phaeophyte alga *Padina durvillaei.* The *Padina* blades provide the major habitat of ***Phyllaplysia padinae.*** This region is also inhabited by 2 other opisthobranch herbivores, *Aplysia californica* (mostly juvenile animals as observed in December 1970) and *Haminoea vesicula* (Gould, 1855). *Padina* is also found below the point where the reef ends abruptly and drops off sharply. The *Padina* blades here are inhabited largely by the sacoglossan *Tridachiella diomedea* (Bergh, 1894). No individuals of *Phyllaplysia* ***padinae*** have been observed here.

The second distinct habitat occurs along the edge of the reef where the substrate is sandy and the supernatant water is shallow. Here, an undetermined species of the marine eel-grass *Zostera* grows rather sparsely relative to the vast beds of *Zostera marina* Linnaeus, on the coasts of



Map of the Sea of Cortez, Mexico

Figure 1

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Dorsal aspect of a 12 mm long animal

Washington, Oregon, and California. Individuals of ***Phyllaplysia padinae*** were encountered crawling about the blades of the eel-grass in this more subtidal habitat.

The individuals of ***Phyllaplysia padinae*** from Puertecitos occurred only on *Padina durvillaei* in the mid-tide zones. Subtidally, the blades of *Padina* revealed no individuals of ***P. padinae*** (as was the case at the type locality) despite the fact that no individuals of *Tridachiella diomedea* were encountered either.

Locomotion: The locomotion of ***Phyllaplysia padinae*** is a distinguishing aspect of many smaller individuals (less than 20mm in length). The initial movement of the animal firmly attached to the algal substrate involves the simultaneous arching of the central portion of the dorsum and the foot while the posterior-most portion of the body is moved forward. The animal then extends forward, returning the body to its dorso-ventrally flattened position. This process is repeated quite rapidly in a continuous cyclical process. This inch-worm-like form of movement was the only noticeable form of locomotion observed in the smaller animals. Actual rates of movement were not calculated, yet relative to other opisthobranchs it appears to be quite rapid and much more so than the common pedal wave action of other animals (see Figure 2).

Larger individuals of ***Phyllaplysia padinae*** (generally over 30mm in length) move in the more conventional method for members of the genus. The anterior portion of the body moves forward first while the posterior half of the body remains stationary until after the elongation of the body and the anterior extension has been completed. Then the posterior section moves forward restoring the animal to its normal resting position as opposed to the full extension that occurs as an intermediate step in this process. At no point does any portion of the foot leave the substrate on which the animal is crawling as is the case with the smaller individuals.

Feeding: Feeding was observed in an aquarium. An individual of ***Phyllaplysia padinae*** collected at Puertecitos grazed upon the surface of *Padina durvillaei*. Grazing is accomplished by the movement of the animal over the algal surface, and the probing of the food substrate by the constant movement of the oral tentacles. The radula is periodically extended to scrape the surface of the algae, thereby ingesting epiphytic diatoms and the epidermal cells of the algae.

Examination of fecal matter from a 37mm long animal kept in the aquarium revealed undigested surface cells of *Padina* together with the siliceous fragments of diatom tests.

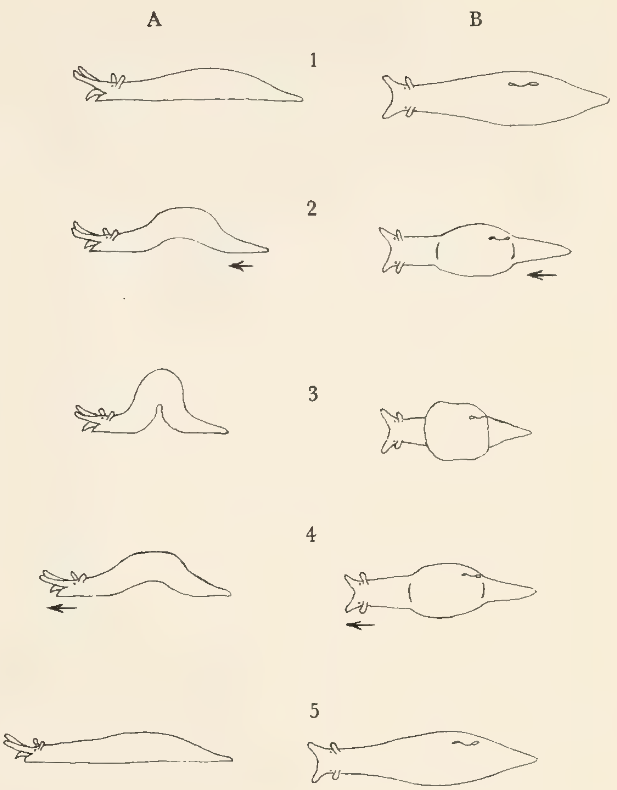


Figure 2

"Inch-worm" mode of locomotion in ***Phyllaplysia padinae*** drawn in linear sequence 1 through 5. A: left lateral view; B: dorsal view; 1: animal in normal position with foot attached to substrate throughout; 2: posterior end of body moves forward (arrow); 3: animal becomes momentarily stationary as dorsal arch reaches maximum height; 4: anterior region of body extends forward, reducing arch (arrow); 5: body returns to normal position as in 1, and process is repeated

Egg Mass: The egg mass of ***Phyllaplysia padinae*** is a flat ribbon found upon the blades of *Padina durvillaei* (see Figure 3). An egg mass collected at Puertecitos measured 7mm in width, 12mm in length, and 3mm in height. Another egg mass found on the inside of a plastic container in which 2 animals were isolated for several days measured 5mm in width, 18mm in length, and 2mm in height. The egg masses are rectangular in shape and of a brownish-green color, quite similar to the color of *Padina*. Three additional egg masses were found at Puertecitos on blades of *Padina,* their maximum length approaching 15mm.

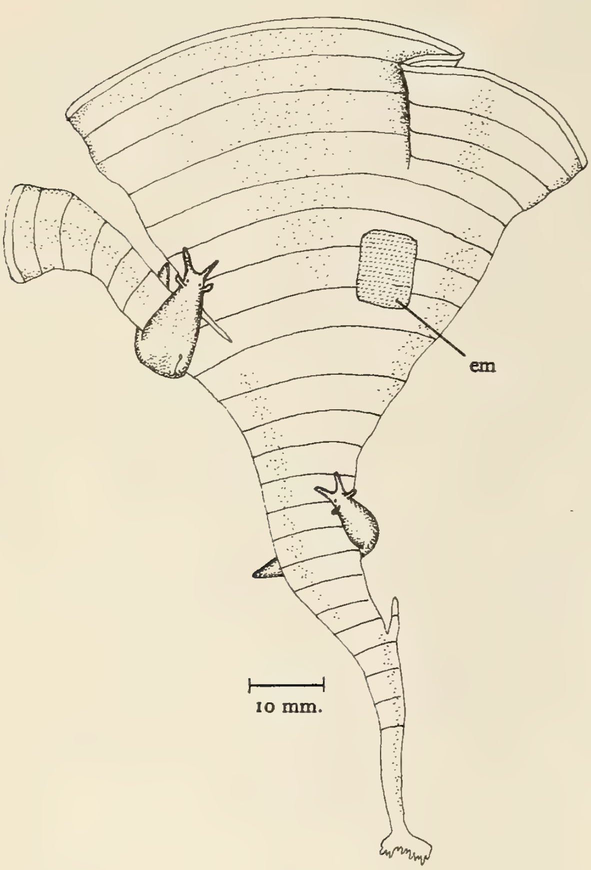


Figure 3

A blade of *Padina durvillaei* with two individuals of *Phyllaplysia padinae* and their characteristic egg mass
em – egg mass

MORPHOLOGY AND ANATOMY

External Characteristics: The ground color of *Phyllaplysia padinae* is olive green to brownish-green with random white spotting of the dorsal surface. The brownish-green ground color is very similar to the color of the host alga *Padina durvillaei.* The foot is brownish-green also, the large digestive gland being readily distinguished through the translucent ventral portion of the body. Several individuals exhibited scattered brown mottling on the dorsal surface; however, the plain green ground color without mottling is most common. The dorsal surface of some animals showed several white star-shaped markings. These markings are small papillae which may be totally absent in some individuals. One animal revealed 8 such papillae near the central portion of the body. The position and number of papillae are purely random, varying considerably in different individuals. The papillae are very variable in shape (Figure 5). The majority are wider than long, and composed of a cluster of small projections from a common base. Less common are papillae of only

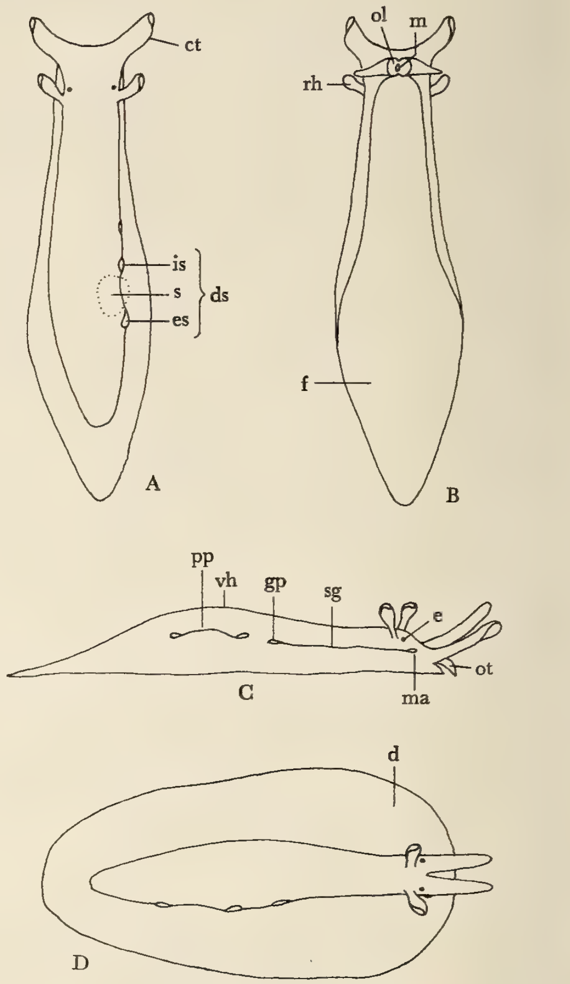


Figure 4

Phyllaplysia padinae Williams & Gosliner, spec. nov.

Diagram of external features: A - dorsal view; B - ventral view; C - right lateral view; D - dorsal view of contracted animal
ct – cephalic tentacle d – dorsum ds – dorsal slit (gill slit)
e – eye es – excurrent (anal) siphon f – foot
gp – gonopore (common genital duct) is – incurrent siphon
m – mouth ma – male aperture (male gonopore)
ol – oral lip (outer lip) ot – oral tentacle pp – parapodium
rh – rhinophore s – shell sg – seminal groove
vh – visceral hump

one tapering individual protuberance, which may be longer than wide. These papillae taper at the ends and do not exceed 0.5 mm in length.

The body shape is typical of the subfamily Dolabriferinae. The foot is broad throughout, though it may vary in shape considerably when the animal is contracted or extended. The body of the animal may exhibit 2 characteristic positions. When the animal is not moving, the body is contracted with the front of the foot protruding in front of the head, with only the cephalic tentacles exceeding the broad anterior region of the foot (Figure 4D). When in this position, the cephalic tentacles are folded together and point straight forward, forming an angle of 180° with the antero-posterior median line of the body. A significant change in shape and size of the body can take place in this non-motile position. A 22 mm long extended animal measured only 18 mm when contracted. Another animal measured 32 mm extended, 26 mm contracted. The largest animal observed measured 45 mm when extended,

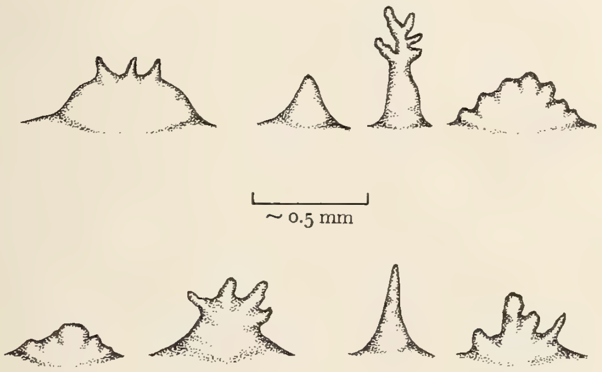


Figure 5

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Variation in dorsal surface papillae

35 mm when fully contracted. When contracted, the body is more elliptic, less elongate. When the animal is moving or in the extended position, the body becomes considerably elongated and narrow, the anterior margin of the foot extends behind the head and the cephalic tentacles spread apart, forming a near right angle between the individual tentacles. When the body is in motion, the foot is widest posterior to the middle of the body (Figures 1 and 4B). When contracted, the foot is widest in the head region, or just anterior to the middle of the body. The living animal is most commonly seen in the extended position and only rarely is the contracted position assumed.

The rhinophores are partially auriculate, typical of the order Anaspidea. They are rather shortened and blunt, slightly club-shaped toward the distal region and cleft approximately $\frac{1}{2}$ of their length. The rhinophores are greenish with white speckling which may form 2 - 4 transverse bands or rings around the central structures. One animal exhibited a reddish-brown speckling forming a transverse ring around the central portion of the rhinophores. Rhinophores in the holotype measured approximately 1 mm in length. The rhinophores originate just posteriorly of the eyes on the dorsal edges of the cephalic region.

The cephalic tentacles are large, thickened structures at the front of the head and cleft their entire length to the base. One animal exhibited a very narrow stripe of white pigment lining the cleft portion of the cephalic tentacles. However, the majority of animals observed showed a uniform green ground color in the cephalic tentacles. The cephalic tentacles in the holotype measured 2.5 mm in length.

The hermaphroditic gonopore is located anteriorly to the front of the gill slit, approximately $\frac{3}{4}$ of the length between the rhinophores and the front of the dorsal slit. The seminal groove, which appears as a thin line leading to the male aperture, arises from the anterior of the gonopore. The male aperture is located just below and in front of the right eye (Figure 4C). The small parapodia form a cavity (the gill slit or dorsal slit) containing the gill and other organs, located slightly to the right of the middle of the body. The incurrent opening lies directly in front of the excurrent opening. The posterior end of the excurrent siphon is located toward the tail of the body, on the posterior slope of the visceral hump. The parapodia are greatly reduced as in other members of the Dolabriferinae. The right parapodium overlaps the left parapodium and covers the middle of the dorsal slit. In the living holotype of *Phyllaplysia padinae* the right parapodium is slightly speckled on its edge with alternating dark and light pigment.

Radula: Inside the buccal mass is contained the tubular horseshoe-shaped radula supported by the basal musculature of the odontophore. The radula is golden brown in color and easily distinguishable when the buccal mass is opened dorsally. The radula is composed of approximately 18 rows of trimorphic teeth. The rachidian column is composed of relatively short teeth, narrow and tricuspid above, broader and bilobed behind. The middle cusp is elongate and pointed at the tip. The 2 adjacent cusps are shorter and rounded, and are equal in shape and size (Figure 6).

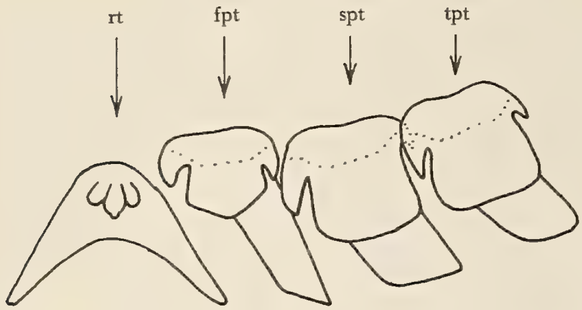


Figure 6

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Radula: elements of 8th half row from right side
fpt – first pleural tooth fopt – fourth pleural tooth
rt – rachidian tooth spt – second pleural tooth
tpt – third pleural tooth

The first lateral column is composed of taller, tricuspid teeth. These teeth are the tallest in the radula and extend slightly above the rachidian and the other lateral teeth. The 3 cusps of the first lateral teeth are blunt and somewhat rounded. The median cusp is slightly angled in the middle, giving rise to 2 relatively straight edges. The 2 adjacent cusps are subequal and rounded at the tips. There exists only 1 column of these teeth on each side of the rachidian column, making 2 such columns in all. The remaining lateral teeth are very wide but shorter than the first laterals. These teeth make up the dominant form in the radula and are relatively uniform in shape and size from the inner to the outer columns. They are also tricuspid with 1 quite reduced, somewhat acute lateral cusp. The inner lateral cusp is larger and varies in shape from a blunt, rounded tip to a relatively tapered, subacute one. The central cusp is very broad with a uniform smooth edge and slight curvature. The bases of these teeth

(adjacent column →)

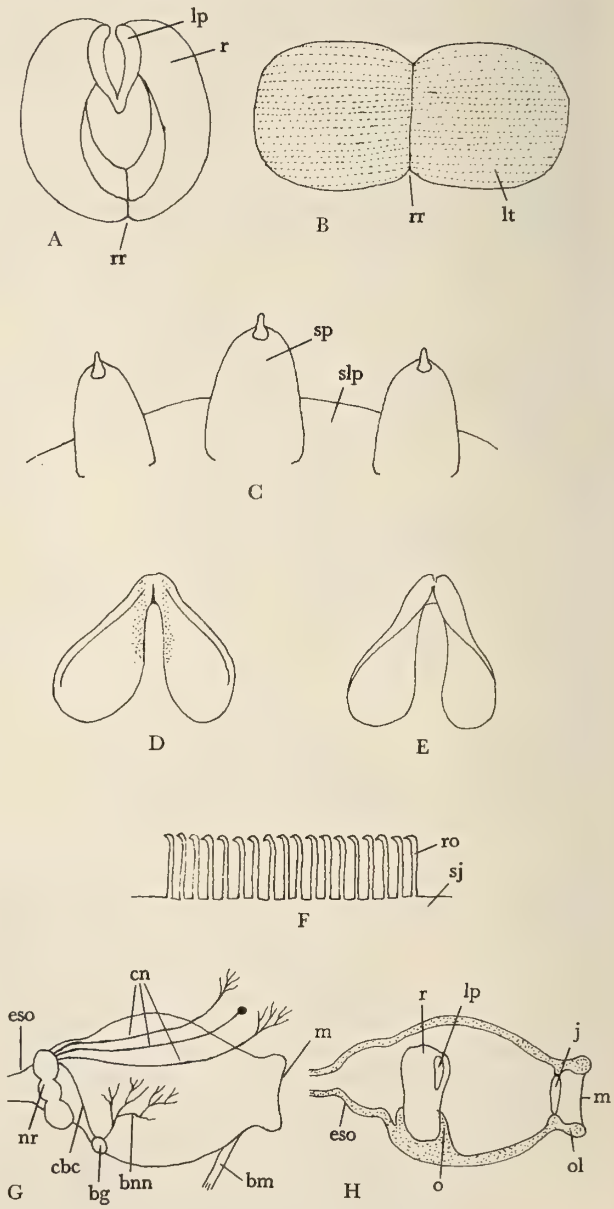


Figure 7

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Elements of the buccal mass
A: anterior view of radula and labial plate; B: the radula as seen flattened on a microscope slide; C: elements of the labial armature (anterior surface of the labial plate); D: jaws, anterior surface (stippling represents area covered with armature); E: jaws, posterior surface; F: elements of the jaw armature; G: right lateral view of buccal mass; H: sagittal section of buccal mass (the anterior is to the right)
bg – buccal ganglia bm – buccal musculature
bnn – buccal nerve network cbc – cerebro-buccal connective
cn – cephalic nerves eso – esophagus j – jaws
lp – labial plate lt – rows of lateral teeth m – mouth
nr – nerve ring (central nervous system) o – odontophore
ol – oral (outer) lip r – radula ro – rodlet
rr – rachidian row sj – surface of jaw
slp – surface of labial plate sp – spine

are quite broad in comparison to the slender elongate basal structure of the first lateral teeth. The lateral teeth may vary in number from 8 to 21 per row. The overall radular formula is therefore $18 \times 8 - 21 \cdot 1 \cdot 1 \cdot 1 \cdot 8 - 21$.

Jaws and Labial Armature: The muscular labial plate forms a V-shaped structure in the dorsal open area of the horseshoe-shaped radula (Figure 7A). This structure is embedded with several tall, mammiform spines with acute apices. These elements comprise the labial armature and line the anterior face of the labial plate.

The jaws are composed of 2 somewhat flattened spoon-shaped plates attached dorsally at their narrow ends. The jaws form an inverted V-shaped structure. The rounded distal ends fold inward creating a tapered funnel-shaped structure as viewed dorsally. The jaws are located within the buccal mass, anteriorly to the radula and just posteriorly to the outer (oral) lip. In addition to the labial armature, the jaws are also densely armed with many tall, narrow rodlets with hooked tips. The area covered with armature extends from the dorsal point of juncture to well down the expanded anterior surface of the jaws (Figure 7D).

Digestive System: The digestive system of *Phyllaplysia padinae* comprises the bulk of the body and extends nearly the full length of the animal. It is composed of 4 main conspicuous regions: the buccal mass, the esophagus, the gizzard, and the digestive gland (Figure 8).

The buccal mass is a globose to slightly elongate muscular structure with longitudinal striations on the outside surface. A sagittal section through the buccal mass reveals its internal structure (Figure 7H). The large radula is positioned on the muscular, basal odontophore. From the opening formed by the curvature of the radula extends the armed labial plate through which begins the esophagus. Just anterior to the radula and labial plate is a thin membranaceous tissue upon which are located the jaws. Anterior to the jaws are the muscular, convoluted outer lip and mouth.

The esophagus forms no definite, easily distinguishable pharyngo-esophageal juncture with the buccal mass. Rather, the esophagus is formed by the gradual tapering off of the buccal area which narrows behind to join with the gizzard. The length of the esophagus does not exceed the length of the buccal mass nor that of the gizzard.

The pharyngeal or salivary glands are relatively wide but elongate organs which join the buccal mass by narrow ducts at the very posterior end of the buccal mass near the beginning of the esophagus.

The gizzard is also a rather globose to somewhat elongate structure, similar in shape to the buccal mass. The gizzard, however, is easily distinguished by a wide band of transversely striated region which encircles the entire median portion of the gizzard (Figure 8). The posterior end of the gizzard tapers rapidly to form a narrow tube which enters the digestive gland. The stomach is that portion of the alimentary tract which is surrounded by the digestive gland. The intestine is then the portion of the tract which exits the stomach and digestive gland to the anus. The anus is located at the posterior opening of the dorsal gill slit (excurrent siphon).

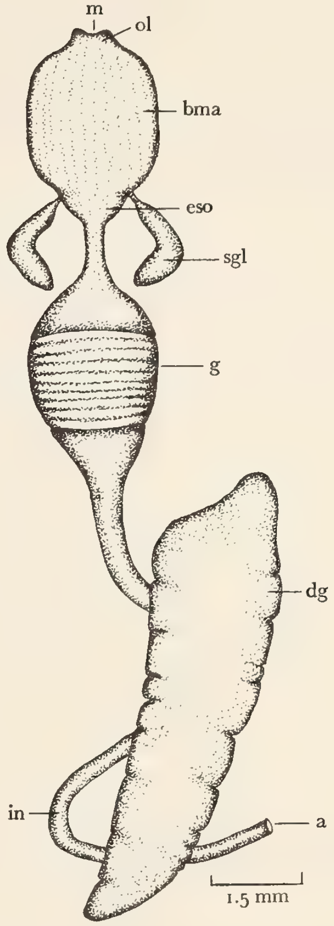


Figure 8

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Dorsal view of digestive system

a – anus bma – buccal mass dg – digestive gland
eso – esophagus g – gizzard in – intestine m – mouth
ol – oral (outer) lip sgl – salivary (pharyngeal) gland

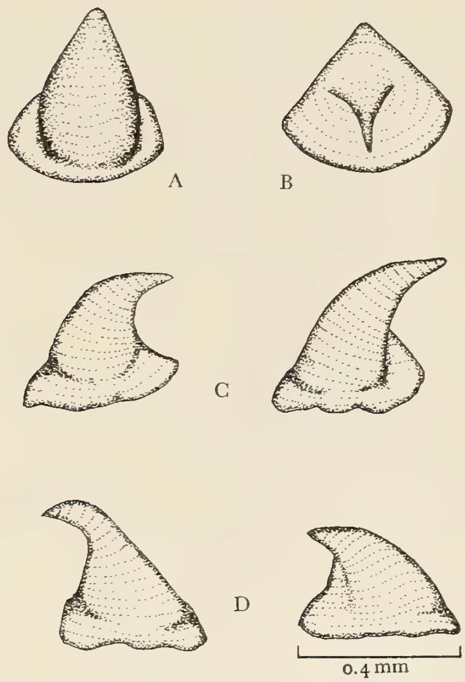


Figure 9

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Gizzard teeth. A: Posterior view; B: dorsal view; C: right lateral view of 2 different teeth; D: left lateral view of 2 different teeth

The digestive gland (liver) is the largest organ in the animal and is associated with the widest portion of the body just posterior to the middle. The digestive gland is deep brownish in color and has a fine granulated texture to its surface. This structure surrounds the stomach and is narrow and tapered at its posterior end. The anterior end is wider, rounded at the corners, and is somewhat concave to fit snugly over the posterior region of the gizzard. The posterior tip of the digestive gland projects into the very posterior portion of the visceral region.

The intestine which comes off from the middle of the digestive gland curves 180° to form a U-shape and exits at the posterior aperture of the dorsal slit (Figure 4A).

Gizzard Teeth: The gizzard of *Phyllaplysia padinae* contains many small gizzard teeth in the inside lining. These structures are cornucopiate in shape (horn-shaped) with a wide, flattened base and pointed apex (Figure 9). Three gizzard teeth from the holotype revealed approximately 15 transverse striations on the curved frontal surface of each. The gizzard teeth are uniform in shape and size, the only exception being that some are more severely hooked at the tips than are others. All gizzard teeth examined measured approximately 0.4 mm in diameter at the base and 0.5 - 0.6 mm in height. In all cases, the height to width ratio was greater than 1.

Shell: The shell of the holotype measured approximately 2 mm in length. A shell removed from a paratype measured about 2.5 mm in length. The shell is strongly built, thickened toward the center. The apex is in the center of the shell, surrounded by numerous concentric rings. The interior of the shell of the holotype is brown and lightly ridged with concentric rings which give rise to the trans-

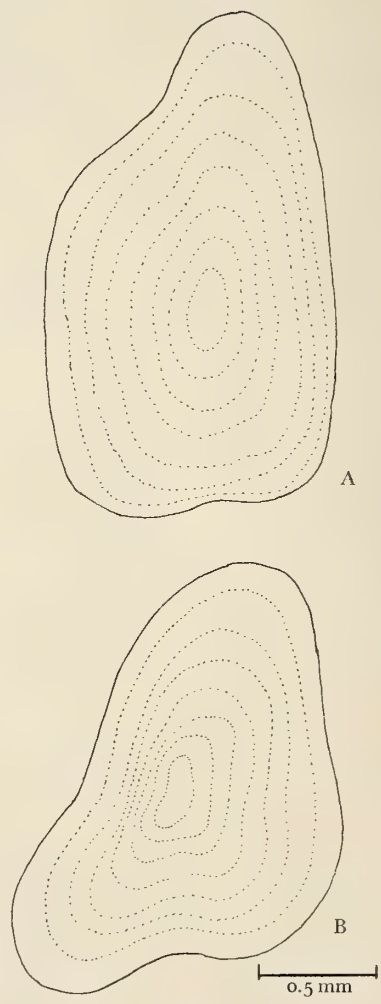


Figure 10

Phyllaplysia padinae Williams & Gosliner, spec. nov.
A: dorsal view of shell of holotype B: dorsal view of paratype shell

lucent, relatively thin outer margin of the shell. The shell, when examined in lateral view, is basically flattened with its highest point in the middle. The shape of the shell is triangular-roundish in outline with 3 usually distinguishable rounded corners. This gives the shell a somewhat elongate appearance (Figure 10).

The shell is contained inside the dorsal slit and is located on the dorsal surface of the mantle shelf.

Respiratory Apparatus: The respiratory organ is a pinnate structure representing a true ctenidium within the dorsal gill slit below the mantle shelf. The ctenidium of the holotype is 1.7 mm in length and is composed of a central mainstem which has a slight clockwise curvature when viewed dorsally. The mainstem has 8 - 9 side branches on each side. Each side branch is surrounded by a thickened U-shaped structure with a small cleft at its distal end (Figure 11). These strucures become progressively larger from the tip to the proximal origin of the ctenidium, giving the gill its tapered appearance. The gill is yellowish in color in living animals.

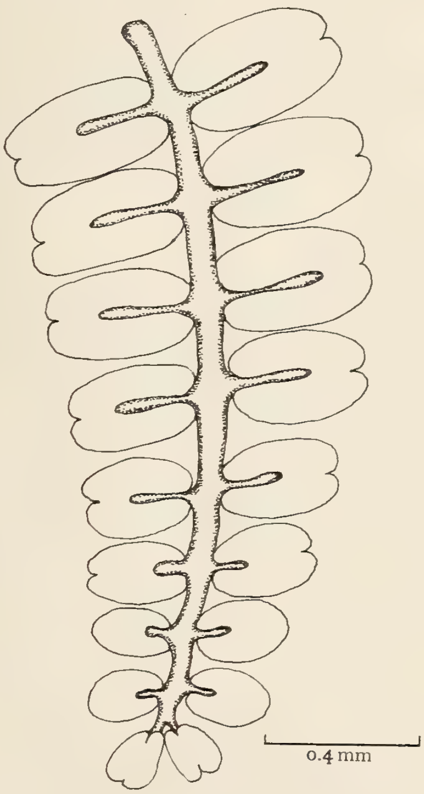
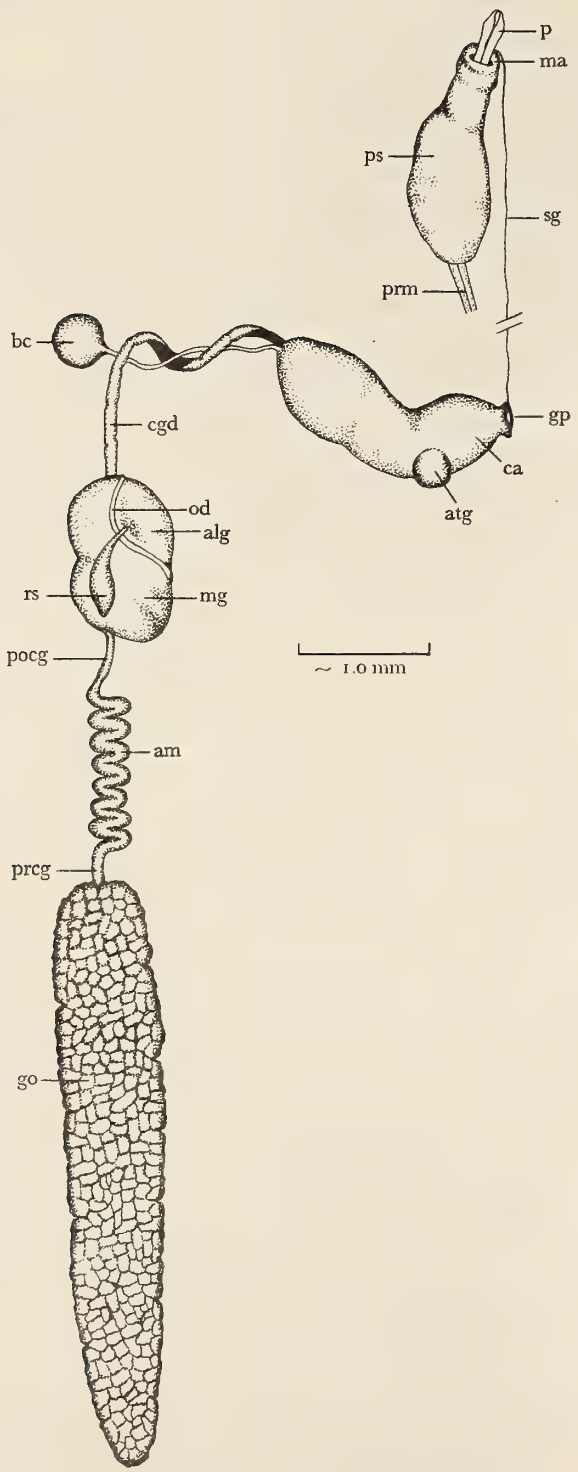


Figure 11
Phyllaplysia padinae Williams & Gosliner, spec. nov.
Dorsal view of ctenidium

Reproductive System: The reproductive system is approximately 6 mm long in the holotype. The pallial gonoduct is a comparatively compact system and is composed of the female gland mass, receptaculum seminis, common atrium, atrial gland, bursa copulatrix, and common genital aperture. The genital opening is located between the gill slit and rhinophore on the right side of the body. From the gonopore extends the common atrium, which is subglobose to elongate in shape. The bulbous atrial gland appears as a small bump near the mid-posterior end of the common atrium (Figure 12). The gonopore is surrounded by a muscular sheath and is located to the right anterior end of the common atrium. From the left anterior region of the common atrium, the tubular portion of the pallial gonoduct, which leads to the female gland mass, parallels the duct of the bursa copulatrix for a short distance. The bursa copulatrix is a spherical organ located at the end of a long and narrow duct. The duct enters directly into the common atrium at its anterior end. In one specimen, the tubular portion of the pallial gonoduct was coiled around the duct of the bursa copulatrix (Figure 12). The posterior portion of the tubular gonoduct leads directly to the female gland mass and is connected to it at the anterior region of the gland mass. The female gland mass is spherical and includes the albumen, membrane, and mucus glands, together with the receptaculum seminis, which emanates from the female gland mass near its middle. The receptaculum seminis is a small club-shaped structure which is conspicuous on the outside of the albumen gland region. From the posterior part of the female gland mass begins the coelomic gonoduct which is composed of the ampulla and gonad. The post-ampullar coelomic gonoduct bridges the ampulla and the female gland mass. From here the ampulla is represented by a tightly coiled tube which is apparent in the posterior region of the reproductive system and leads via the pre-ampullar gonoduct to the gonad. The ovotestis is the largest organ in the reproductive system and in the holotype measures approximately 3 mm in length. Its outside surface is granular in texture and is composed of well over a dozen individual follicles. The gonad is elongate and tapers slightly toward its posterior end.

Male Copulatory Apparatus: From the female gonopore the narrow, ciliated seminal groove can be seen as a thin line on the external surface of the body; this is on the right side of the animal and comprises the only connection between the main reproductive system and male



copulatory apparatus. The male gonopore is located just ventrally from the eye and to the right of the rhinophore (Figure 4C). The male copulatory apparatus is composed superficially of a highly muscular and striated penial sheath and shortened penial retractor muscle (Figure 13A). The penial sheath is sacklike in shape with a long tapering neck which exits from the body at the male aperture. The uncontracted sheath in the holotype measured about 3 mm in length. Inside the penial sheath is contained the contractile penis. The penis is characteristically cleft on its dorsal side from the distal tip to less than $\frac{1}{2}$ its length. The penis, contracted in the holotype, measured 0.4 mm in width at the tip and 1.2 mm in length. On both sides of the cleft are embedded up to 5 penial spines which are arranged in 2 relatively uniform rows (Figure 13D). These spines are somewhat variable, but always mammiform and measure approximately 0.1 mm in diameter at the base. Their height may vary from 0.1 to 0.3 mm. The spines are broad at the base and taper to form acute and elongate tips (Figures 13F to 13I).

Nervous System: The nervous system is composed of 10 major ganglia, all centralized near the anterior nerve ring surrounding the esophagus. On the dorsal surface of the esophagus can be seen the large, paired cerebral ganglia. These are connected together by the thickened cerebral commissure. The diameter of one cerebral ganglion is approximately equal to the length of the cerebral commissure. On the latero-ventral side of the cerebral ganglia and on the sides of the esophagus are the pleural ganglia which are connected to the cerebral ganglia by an extremely short, not easily distinguishable cerebro-pleural connective. To the inward lateral sides of the pleural ganglia arise 2 small rounded ganglia (Figure 14). These are the visceral-subintestinal-parietal ganglion on the left and the supraintestinal-parietal ganglion on the right. These ganglia are attached to the pleural ganglia by respective connectives. From each of these ganglia arise elongated nerves which extend into the posterior part of the body and branch at their ends. At the ventral-most region of the central nervous system are located the large pedal ganglia. The thickened pedal commissure which connects the 2 ganglia forms the ventral part of the nerve ring. From each of the pedal ganglia arise several long pedal nerves which extend into the foot region and ventral viscera. The pedal and pleural ganglia are connected by the pleuro-pedal connective which is short and difficult to distinguish. The cerebro-pedal connectives are very difficult to distinguish since the position of the pleurals bridges the 2 ganglia and makes observation of the direct connective between the cerebrals and pedals obscure. From the antero-dorsal region of the cerebral ganglia

(← on facing page)

Figure 12

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Dorsal view of reproductive system (not drawn to scale)
alg – albumen gland am – ampulla atg – atrial gland
bc – bursa copulatrix ca – common atrium
cgd – common genital duct go – gonad (ovotestis)
gp – gonopore (common genital duct) ma – male aperture
mg – mucus gland od – oviduct p – penis
prm – penial retractor muscle ps – penial sheath
psp – penial spine sg – seminal groove

arise the cerebro-buccal connectives which form the link between the cerebral and buccal ganglia. Also from this region arise several cephalic nerve networks which include the tentacular, rhinophoral, and optic nerves. These nerves may branch at their ends and extend into the anterior cephalic region of the animal. From the buccal ganglia extend the branched networks of the buccal nerves which surround part of the lateral surface of the buccal mass (Figure 14). The buccal ganglia are located at the ventral portion of the bucco-esophageal juncture, adjacent to the postero-ventral region of the buccal mass.

DISCUSSION

Generic Discussion: The subfamily Dolabriferinae contains 3 known genera: *Dolabrifera* Gray, 1847, *Petalifera* Gray, 1847, and *Phyllaplysia* Fischer, 1872. The subfamily is distinguished from other anaspideans by the small, flattened, rounded to spatuliform shell without a strongly curved apex. Often the shell is totally absent. Also in dolabriferans, the parapodia are greatly reduced and as Beeman (1968: 94) describes: "parapodia separated anteriorly by genital groove, broadly joined poste-

(adjacent column →)

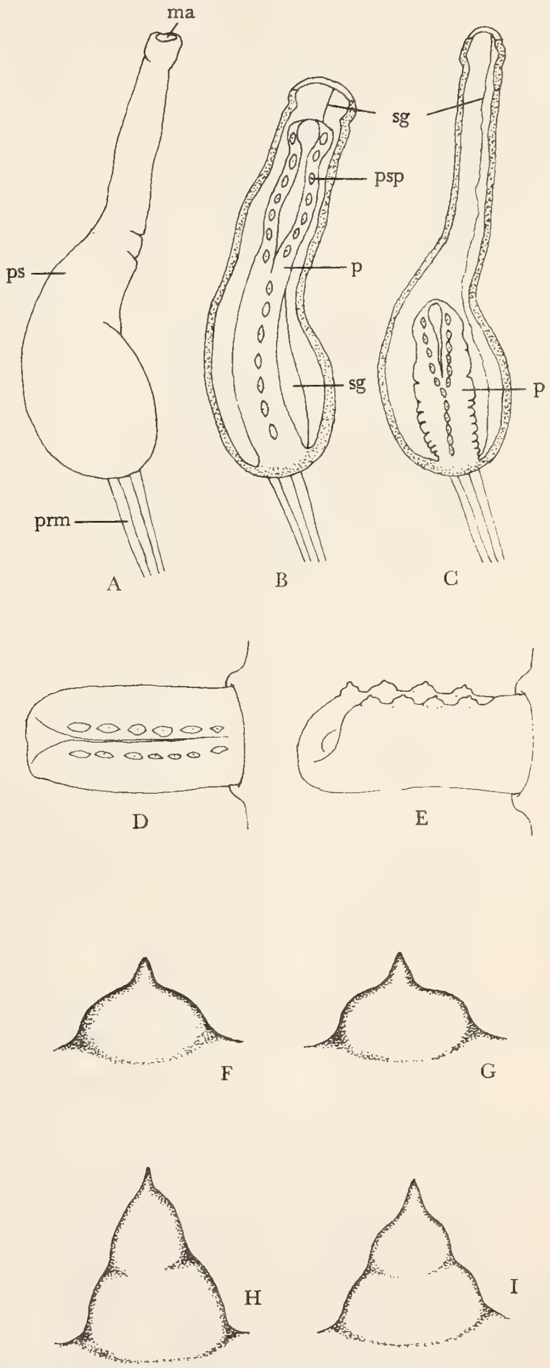


Figure 13

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Male reproductive structures
A: dorsal view of male reproductive system; B, C: dorsal half of penial sheath removed; B: penis partially extended; C: penis contracted; D: dorsal view of tip of penis; E: left lateral view of tip of penis; F to I: variation in penial spines
ma – male aperture (male gonopore) p – penis
prm – penial retractor muscle ps – penial sheath
psp – penial spine sg – seminal groove

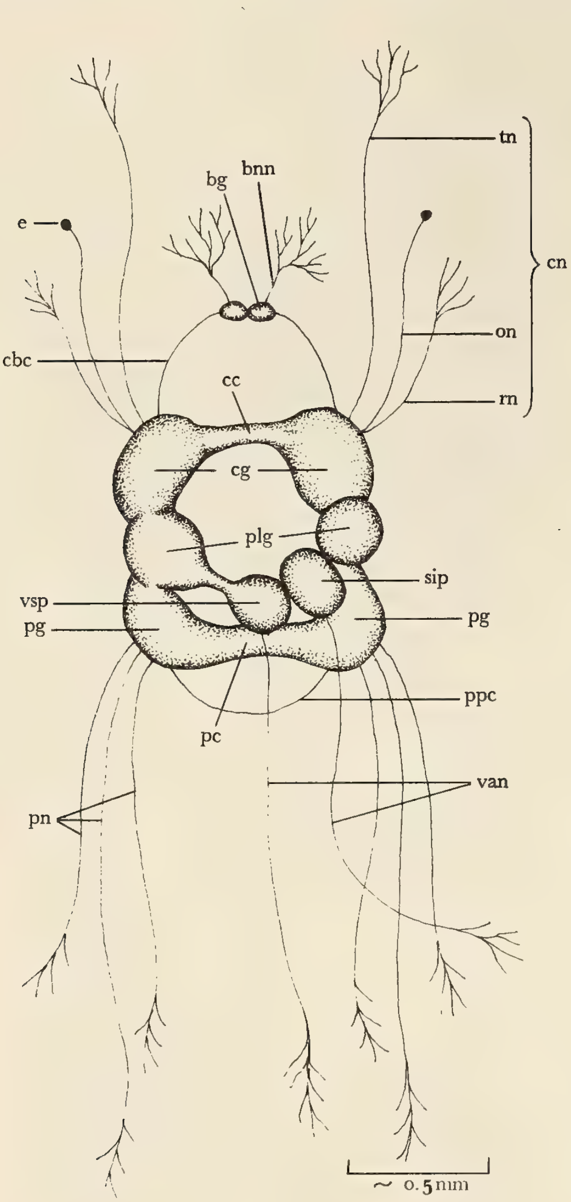


Figure 14

Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Ventral view of nervous system

bg – buccal ganglion bnn – buccal nerve network
cbc – cerebro-buccal connective cc – cerebral commissure
cg – cerebral ganglia cn – cephalic nerves e – eye
on – optic nerve pc – pedal commissure pg – pedal ganglion
plg – pleural ganglia pn – pedal nerves
ppc – parapedal commissure rn – rhinophoral nerve
sip – supraintestinal-parietal ganglion tn – tentacular nerve
van – viscero-abdominal nerves
vsp – visceral-subintestinal-parietl ganglion

riorly, small, not freely motile, often asymmetrical and displaced to the right." The subfamily Dolabriferinae can be distinguished readily from the subfamily Aplysiinae by the greatly shortened visceral loop in the nervous system. As a general rule, anaspideans or other opisthobranchs with well developed motile parapodia have greatly extended visceral loops with posterior ganglia separated from the central nervous system. The regionalization of nervous tissue in this manner consequently allows for decentralized control and greater flexibility in a given area of the body. In this case the nervous control for the extremely well developed, highly motile parapodia in the genus *Aplysia* are directed by a posteriorly located nervous tissue concentration composed of 2 ganglia represented by fusions between the left parietal, subintestinal, and visceral ganglia on the left and the right parietal and supraintestinal ganglia on the right (Figure 15A). In dolabriferans, such as *Phyllaplysia,* the visceral loop has virtually disappeared and the 2 posterior ganglia have migrated to the central nervous system where they are present between the pleural ganglia adjacent to the pedal commissure (Figure 15B). The effect of this migration can be seen externally by the greatly reduced non-motile parapodia.

The distinctions between the 3 dolabriferan genera have been shrouded in confusion in much of the literature. The genus *Dolabrifera* can be separated easily from the others by the presence of a slender elongate shell with terminal knobbed spire and greatly broadened posterior $\frac{1}{3}$ of the body (Beeman, 1968:94). The species *Dolabrifera dolabrifera* (Rang, 1828) is known virtually worldwide from the tropics and has recently been recorded by Bertsch (1970: 110) from Las Cruces Bay, Baja California, in the Gulf of California, and from the Galápagos Islands by Sphon & Mulliner (1972: 149).

Distinctions between the other 2 dolabriferan genera, *Phyllaplysia* and *Petalifera,* are representative of the confusion within the Dolabriferinae. Hyman (1967: 607) states that in *Petalifera* the shell is present and is entirely wanting in *Phyllaplysia.* However, several established species of *Phyllaplysia* are known to possess shells. Marcus (1955: 55) illustrates the shell of *Phyllaplysia engeli* (fig. 4 of that work). Beeman (1968: plt. 11, fig. 2) shows a photograph of the secondary shell of *Ph. taylori.* The shell of *Ph. padinae* is diagrammatically represented in Figure 10. Beeman (*op. cit.*: 94) states that a shell has also been reported by Bergh (1905) for *Ph. inornata* Bergh, 1905. Because of these citations the mere presence or absence of a shell cannot be used as a taxonomically valid factor in differentiating between *Petalifera* and *Phyllaplysia.* Further confusion has also been added in regard to radular characteristics. In the diagnosis of the

genus *Phyllaplysia* P. FISCHER (1872: 296) describes the radular teeth as tricuspid ("*dentes linguales tricuspidati, obtusi, non aculeati*"). THIELE (1931: 395 - 399) describes the rachidian teeth of the genus *Petalifera* to be 5-cusped (" ..., Schneide mit 5 Zähnen, ... ") and *Phyllaplysia* to be tricuspid ("..., mit dreizackiger Schneide, ...). This would seem to be an easy way to distinguish the 2 genera, except for the fact that *Ph. paulini* Mazzarelli, 1895, *Ph. viridis* (Bergh, 1905), *Ph. varicolor* (Bergh, 1905), and *Ph. taylori* Dall, 1900 all have 5 cusps on the rachidian teeth (and sometimes 7 in *Ph. viridis*). Because of these exceptions the number of cusps on the rachidian teeth also cannot be used as a taxonomic criterion to distinguish the 2 genera.

There are valid characters, however, which are important in distinguishing between the genera *Petalifera* and *Phyllaplysia*. These are concerned with shell structure and foot characteristics. BABA (1959) recognizes only 4 species of *Petalifera*. These are *Pe. petalifera* (Rang, 1828), from the Atlantic and the Mediterranean, *Pe. albomaculata* (Ferran, 1905) of the Indian Ocean, *Pe. punctulata* (Tapparone-Canefri, 1874) from Japan, and *Pe. ramosa* Baba, 1959, from Japan and Florida. All the above listed species of *Petalifera* possess thin shells with terminal apices at one end and crescent-shaped concentric rings emanating outward from the apex. In all species of *Phyllaplysia* possessing a shell the apex is in the middle of the shell, with concentric circles surrounding the apex and extending out toward the margins of the shell (see Figures 15C to 15E for comparison). This basic difference in shell structure seems to be a valid criterion for the taxonomic distinction between the 2 genera.

Also to be considered is the attachment of the anterior region of the foot with the body margin. MARCUS (1957: 53) in describing *Phyllaplysia engeli* states: "the anterior border of the foot is occasionally bilabiate. Also, in these cases, it is connected with the lateral margins of the body, so that the difference against *Petalifera* with free anterior border of the foot (Engel, 1936, p. 48; Engel and Hummelinck, 1936, p. 48) continues to be valid." In individuals of *Ph. taylori* and *Ph. padinae* observed by us, the anterior margin of the foot and the body margin are attached throughout.

Ecology and Distribution: Of the 12 species of *Phyllaplysia*, only 2 other than *Ph. padinae* are known from the coasts of North and South America. *Phyllaplysia engeli* is found from the coast of Florida, throughout the Caribbean, to the northern sector of the State of Saõ Paulo, Brazil. *Phyllaplysia taylori* occurs along the Pacific coast of North America from Vancouver Island, British Columbia, to San Diego, California. No species of *Phyllaplysia* appears to have a worldwide, hemispherical or circumtropical distribution and apparently none occurs on more than a single coastline of a single ocean. *Phyllaplysia padinae* is the first member of this genus recorded from the Panamic province.

While the genus *Phyllaplysia* includes distributionally quite disjunct species, certain facts about their substrates and feeding habits remain fairly constant. *Phyllaplysia* is known only from 2 habitats, crawling on the marine grasses of the genus *Zostera* and from the phaeophyte *Padina*. Both of these genera have worldwide distributions, *Padina* in the tropics and *Zostera* in the more temperate waters. *Phyllaplysia padinae* is the only species recorded from both substrates. *Phyllaplysia taylori* and *Ph. lafonti* are known on *Zostera* and *Ph. engeli* is known on *Padina*. The substrates on which the other species occur have not been recorded. While the substrate is well known, the actual food source for members of the genus has been the subject of much confusion. MACFARLAND (1966) stated that *Ph. taylori* feeds on bryozoan colonies found on the blades of *Zostera marina* Linnaeus. FISCHER (1870) stated that *Ph. lafonti* feeds on *Zostera* and algae. BEEMAN (1968) noted that *Ph. taylori* in fact feeds on epiphytic diatoms found on the blades of *Zostera*. Our examinations of fecal matter from central Californian individuals of *Ph. taylori* have revealed that the primary food source of this species is the diatom *Isthmia nervosa* Kütz. MARCUS (1957) adds to this knowledge by mentioning that diatoms were found in the stomach and intestine of *Ph. engeli*. Fischer's report that *Ph. lafonti* feeds on *Zostera* is perhaps more incomplete than erroneous. In *Ph. padinae* the first cell layer of the polystromatic alga *Padina durvillaei* is scraped off as the animal grazes along the blades. The bulk of the epidermal surface cells of *Padina* which are ingested pass through the gut undigested, while the contents of most of the epiphytic diatoms are digested and their tests egested after being ground by the gizzard. This is most likely what occurs in *Ph. lafonti* as it grazes on *Zostera*.

External Characteristics: General body shape and structure are relatively uniform throughout the 12 species of *Phyllaplysia*. Body length of the described species is also quite uniform; most are under 50mm in length; only *Ph. taylori* is known to exceed this length materially.

Although general shape and size are basically uniform throughout the genus, color patterns do vary considerably. However, most species have been described as having a greenish ground color. *Phyllaplysia plana* is green decorated with yellow and pink spots; *Ph. engeli* is often rusty brown with a greenish hue and sometimes with pinkish mottling; *Ph. taylori* is described by BEEMAN (1968: 99)

as having a bright green ground color with distinct dark striping; *Ph. ornata* is dark green with yellow spots, while *Ph. paulini* is light green with white longitudinal lines; *Ph. lafonti* is green with white and grey spots surrounded by violet. *Phyllaplysia padinae* is olive green with random white spots, and *Ph. viridis* is green throughout with branched dorsal processes; lastly, *Ph. varicolor* is greyish to reddish brown with white dots.

Digestive System: The digestive system of most members of the genus *Phyllaplysia* is uniform in structure and shape. It consists of the buccal area, an esophagus, 2 salivary glands, a gizzard with an anterior and posterior portion, a stomach, a large digestive gland, an intestinal tract and an anus at the opening of the pallial cavity. The radula and jaws are of great taxonomic importance and will be considered first.

The jaws in all species of *Phyllaplysia,* where described, have many hook-shaped elements. In *Ph. engeli* these elements are curved with little or no recurving at the apices. In *Ph. padinae* the apices of the rodlets show considerably more recurving than in *Ph. engeli.* The number of elements of the jaw is not readily ascertainable, and it is extremely difficult to establish differences between species.

The numbers of radular teeth and cusps are probably the most readily quantifiable characters of most mollusks. In *Phyllaplysia* the radula is extremely variable on the interspecific level, and thus is significant in the determination of the taxonomy of the genus. *Phyllaplysia* may have a rachidian plate with either 3, 5 or 7 denticles. *Phyllaplysia padinae* has 3 denticles on its rachidian plate; only *Ph. engeli, Ph. lafonti,* and *Ph. depressa* share this particular characteristic (compare Figures 15K to 15M). ENGEL (1936) considers *Ph. depressa* to be identical with *Ph. lafonti,* but does not provide a formal synonymy.

The buccal mass in *Phyllaplysia padinae* is simply ovoid in shape. Most other species of the genus share this trait. In *Ph. engeli* the buccal mass is ovoid at the anterior end, while the posterior $\frac{2}{3}$ of the mass is decidedly rectangular in shape.

The gizzard teeth in *Phyllaplysia padinae* are cornucopiate in shape. In *Ph. engeli* these teeth are described as being pyramidal in shape. The teeth in *Ph. engeli* are blunt, stout structures which lack the obvious curvature of those in *Ph. padinae* (compare Figures 15I and 15J).

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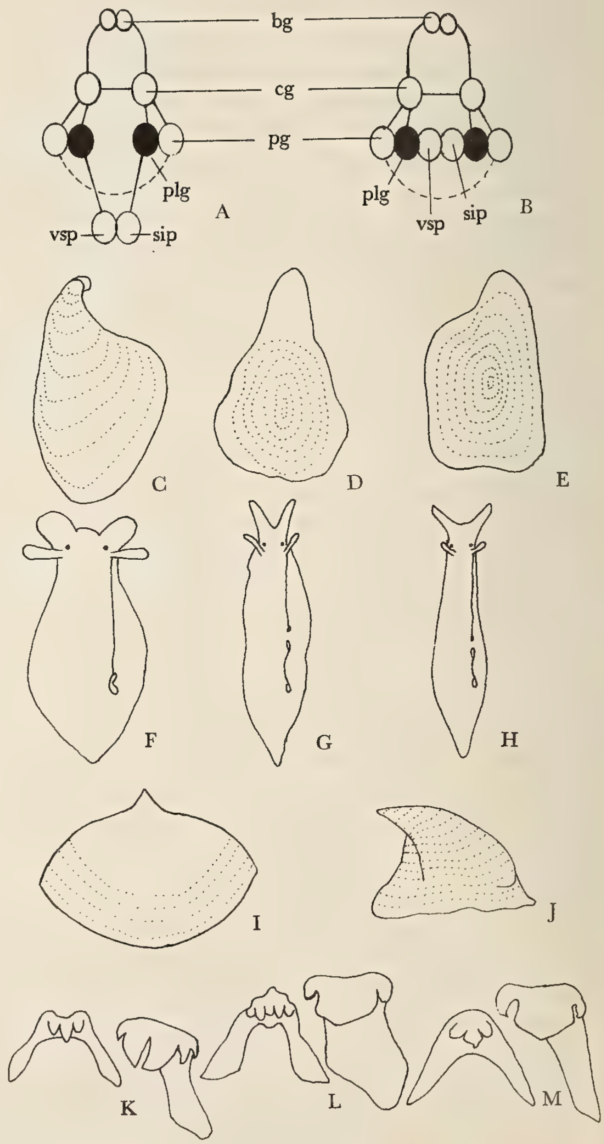

Figure 15

Comparative anatomical diagrams

A: schematic diagram of the nervous system in the Aplysiinae; B: schematic diagram of the nervous system as seen in the Dolabriferinae; C: shell of *Petalifera ramosa* (after MARCUS & MARCUS, 1967); D: shell of *Phyllaplysia engeli* (after MARCUS & MARCUS, 1957); E: shell of *Phyllaplysia padinae*; F: body outline of *Phyllaplysia engeli*; G: body outline of *Phyllaplysia taylori*; H: body outline of *Phyllaplysia padinae*; I: gizzard tooth of *Phyllaplysia engeli*; J: gizzard tooth of *Phyllaplysia padinae*; K: rachidian and first lateral tooth of *Phyllaplysia engeli*; L: same teeth from radula of *Phyllaplysia taylori*; M: same teeth from radula of *Phyllaplysia padinae*

bg – buccal ganglia cg – cerebral ganglia pg – pedal ganglion
plg – pleural ganglia sip – supraintestinal-parietal ganglion
vsp – visceral-subintestinal-parietal ganglion

The digestive gland is the largest organ in the body of *Phyllaplysia* and comprises a substantial portion of the posterior portion of the body. In the genus the gland takes the shape of the body itself. In *Ph. padinae* the body is fairly slender and elongate, hence the digestive gland is long and slender; in *Ph. engeli* the body is much stouter and the digestive gland also assumes that form (Figures 15F to 15H).

Reproductive System: The reproductive system of *Phyllaplysia* provides a good basis for taxonomic distinction. Various differentiable aspects of the reproductive organs will be discussed.

Most obvious externally is the common genital aperture. Its position is variable between species and is very valuable in taxonomic determination. In *Phyllaplysia lafonti* the aperture is within the parapodial slit, while in *Ph. engeli* it is outside the parapodial cavity, immediately adjacent to the anterior border of the slit. In both *Ph. taylori* and *Ph. padinae* the genital opening is approximately $\frac{1}{3}$ of the way between the anterior end of the parapodial slit and the head, considerably anterior to the positions of either of the species mentioned above.

Internally, the second largest organ is the gonad or ovotestis. BEEMAN (1970) states that whether this organ is lobate or non-lobate depends largely on the state of preservation or degree of dissection. With this we would agree; however, the degree to which this occurs is variable. In *Phyllaplysia engeli* about a dozen follicles occur which are completely distinct from each other. In *Ph. padinae* and *Ph. taylori* the ovotestis appears as a solid mass and even in its dissected state the lobes are by no means completely distinct from each other. In *Ph. engeli* the ovotestis mass is short, while in both *Ph. padinae* and *Ph. taylori* the mass is a very dense, elongate structure.

In *Phyllaplysia padinae,* as well as in *Ph. taylori,* the ampullar region is long and consists of many coiling convolutions. In contrast is the ampulla in *Ph. engeli,* where this structure is very short and shows only a minute amount of coiling.

In *Phyllaplysia padinae* the bursa copulatrix opens directly into the common atrium via an elongate tube. This is in contrast wtih both *Ph. engeli* and *Ph. taylori*; in both of these species the bursa empties into the common genital duct rather than into the atrium. The unusual coiling of the genital duct around the tube of the bursa copulatrix also appears to be unique to *Ph. padinae* (Figure 12).

The penis in most species of *Phyllaplysia* varies substantially. MARCUS (1955 and 1961) adds some confusion to the situation. In his 1955 paper he states quite correctly that *Ph. plana* lacks spines on the penis itself. In 1961 (p. 12) he states: "A smooth penis does not seem to occur in *Phyllaplysia.*", without making any further reference to *Ph. plana.* Apparently, *Ph. plana* is the only species of described *Phyllaplysia* that lacks spines on the penis. The penis of *Ph. padinae* is unique in its structure in that it is cleft at the tip. This structure has not been recorded previously for *Phyllaplysia* (Figure 13B).

Nervous System: Significant changes have taken place in the nervous system of *Phyllaplysia* which distinguish it from the idealized primitive opisthobranch proposed by GUIART (1901) (see also BULLOCK & HORRIDGE, 1965). In *Ph. padinae* the nervous system is extremely compact, with all the ganglia contained in the nerve ring surrounding the esophagus. The visceral loop has been shortened (as discussed above under generic discussion), and important ganglionic fusions have taken place, thus concentrating nervous tissue and assimilating it in the central nervous system. On the left side, the visceral, subintestinal, and left parietal ganglia have fused. This has resulted in one ganglion, which has become situated on the nerve ring to the inside of the pleural ganglion. On the right side, the supraintestinal and right parietal ganglia have fused; this also has resulted in one ganglion which has become situated to the inside of the right pleural ganglion. The representative 2 ganglia of these fusions of formerly 5 ganglia are situated adjacent to one another on the inside ventral portion of the nerve ring (Figure 14).

In *Phyllaplysia padinae* the cerebral commissure length is about equal to the diameter of one ganglion of the cerebral ganglia. In *Ph. engeli* the commissure is much smaller than the diameter of a single ganglion. The 2 ganglia making up the cerebral ganglia are therefore in very close proximity to each other, almost touching, whereas in *Ph. padinae* they are separated to a considerable degree.

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Observations on the Attachment of Egg Capsules to a Substrate by *Melongena corona*

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(14 Text figures)

INTRODUCTION

THE NEOGASTROPODA (superfamilies Muricacea, Buccinacea, Volutacea, Conacea) in general lay their eggs in substantial disk- or vase-shaped capsules attached singly or in groups to a substrate. A number of fertilized eggs imbedded in an albuminous fluid enter the capsule gland and are there enclosed in a single soft capsule. Such soft capsules are then passed out of the gonopore and transported externally to a ventral pedal gland. This gland orients, moulds, and hardens the capsules, and is involved with attaching them to a substrate.

FRETTER (1941) describes the morphology and function of the gland in several snails but does not relate an actual temporal sequence of events in capsule deposition.

The passage of egg capsules into the ventral pedal gland has also been observed by: ANKEL (1929) in *Nassarius*; RISBEC (1935) in *Charonia*; DULZETTO (1950) in *Murex*; and MIYAWAKI (1953) in *Neptunea*. Egg capsules remain in the pedal gland in these species for periods ranging from several minutes to several hours.

MAGALHAES (1948) noted that *Busycon carica* produced 6 - 7 egg capsules per 12-hour period.

Egg capsule production in *Melongena corona* (Gmelin, 1791) has been observed by CLENCH & TURNER (1956) who note capsule numbers, sizes and eggs contained per capsule, but do not comment on the actual deposition of egg capsules.

HATHAWAY & WOODBURN (1961) found 49 rows of egg capsules of *Melongena corona* to be composed of from 6 to 20 capsules each. They found a mean value of 12 capsules per row.

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The observations related here were made on a single specimen of *Melongena corona* during 2 egg laying periods. The specimen, of 46.1 mm shell length, had been captured on a rocky intertidal flat at Conch Key, Florida Keys, Florida. It had, prior to egg laying, shared an ambient salinity (31 - 35‰), controlled temperature (constant 31° C) tank with running seawater, with 2 other female and 3 male specimens for some 13 months. Temperatures of 31° C or higher are not unusual for the locality at which the specimen was collected. We suspect that the temporal scale noted here might have been modified to some degree by the laboratory conditions in which the snail was living before and during the time of spawning. The sequence of events probably remained as it would have been in the field.

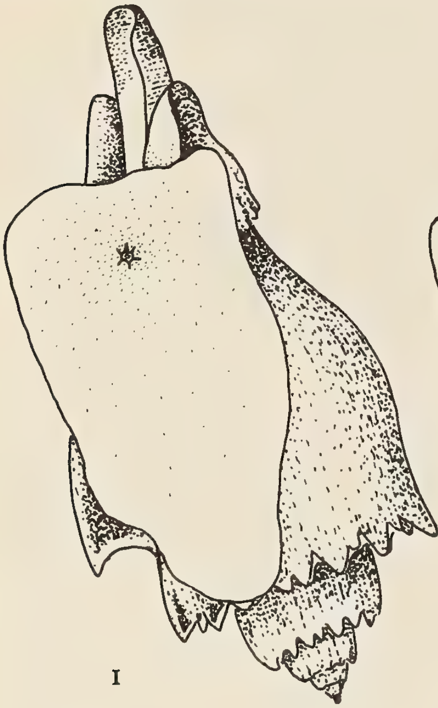
OBSERVATIONS

Egg capsule production and attachment by *Melongena corona* were observed in the laboratory, through the clear glass side of an aquarium, on May 9, 1972.

The appearance of the pedal sole of the female specimen of *Melongena corona,* during activities other than egg laying and, in this instance, just before egg laying, is illustrated in Figure 1. The ventral pedal gland may be noted in the anterior portion of the pedal sole.

The activity which we call a "pedal lick" is shown in its beginning stages in Figure 2 and a few seconds later in Figure 3. This action may serve one or several purposes, among them possibly the determination of substrate suitability for egg capsule attachment, the preparation of the substrate for egg capsule attachment, and the measurement of distance between successive egg capsules. The pedal lick requires only 30 seconds to complete.

In Figure 4, the snail's pedal sole is shown to be more or less inactive. This condition lasts from 2 - 4 minutes



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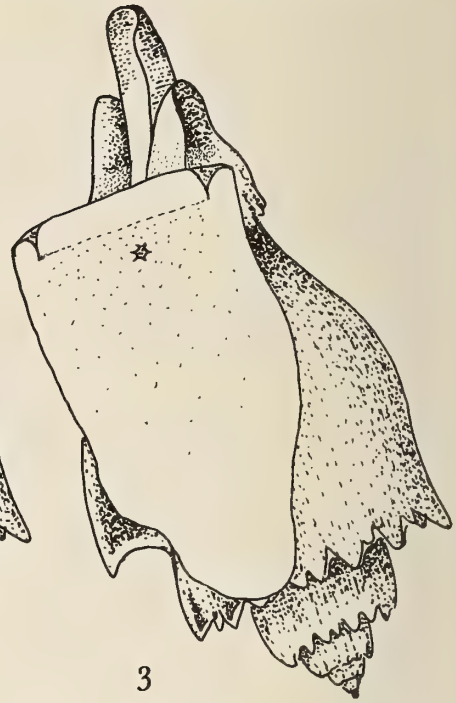

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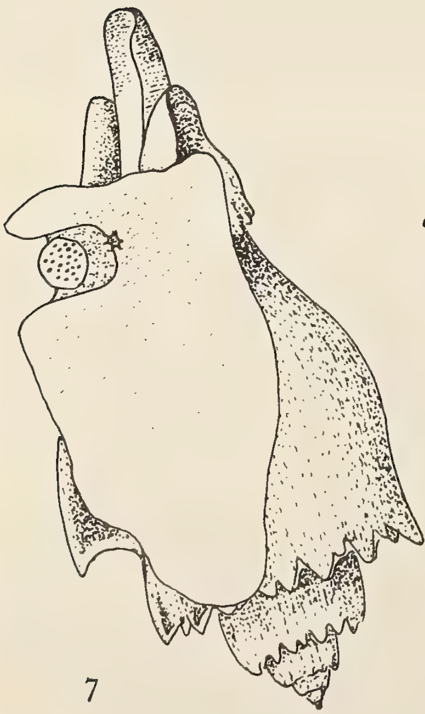

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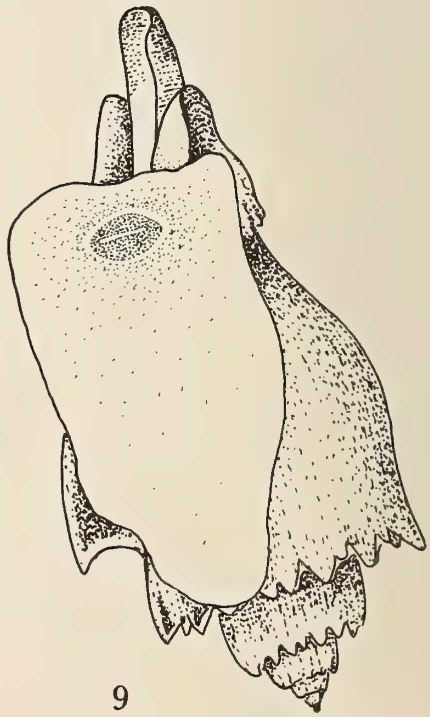

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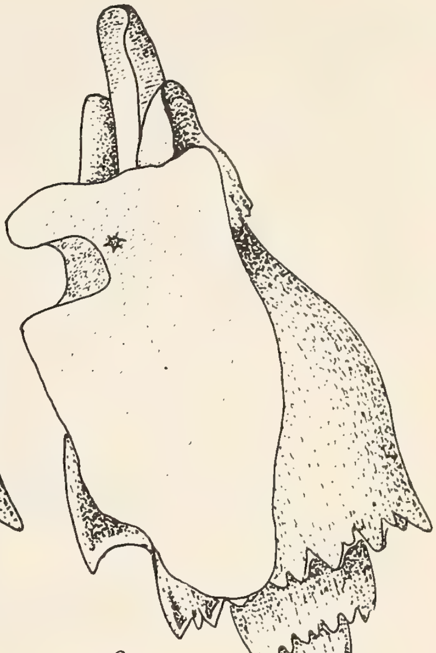

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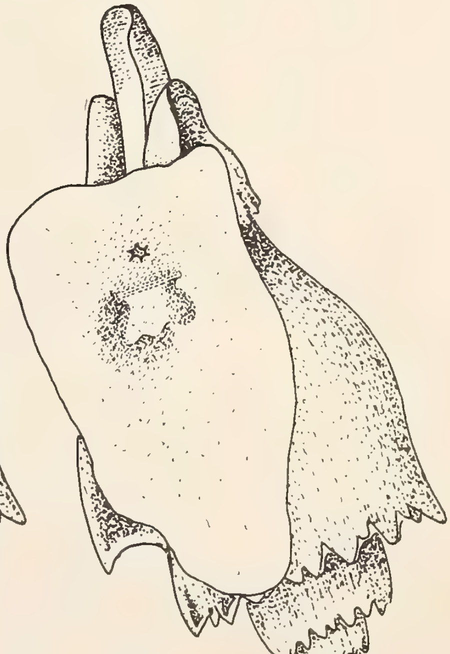

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and averages 3 minutes in duration before a constriction on the antero-lateral portion of the foot (Figure 5) becomes evident. The constriction quickly becomes a well formed groove (Figure 6) and within seconds a roundish packet of eggs is seen to move through the groove (Figure 7) and into the ventral pedal gland (Figure 8). About one minute is required for this action.

The soft egg capsule is quickly oriented within the pedal gland and its base pressed against the substrate. The appearance of the pedal gland during this period (34 - 40 minutes) is illustrated in Figure 9. The snail then appears to pull away from the attached egg capsule. The capsule is bent back under the foot with its dorsal edge remaining slightly hidden by the pedal sole (Figure 10). About 2 minutes are taken for the expulsion of the egg capsule. The snail remains motionless for approximately 2 minutes after the egg capsule is expelled. A pedal lick (Figure 11) which ends with a slight movement forward (Figure 12) initiates subsequent series of events that culminate in egg capsule attachment.

Seven full series of these events were observed. The total time from pedal lick to pedal lick (time per egg capsule) was 45 ± 1 minutes. The temporal schedule is presented in Figure 13.

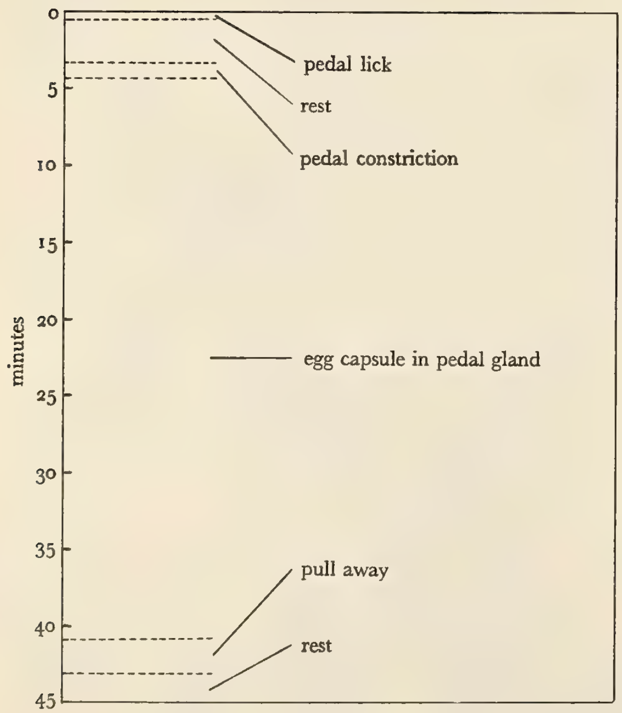

Figure 13

Temporal schedule of events in egg capsule attachment in *Melongena corona*.

On June 26, 1972, the specimen whose egg laying habits have already been discussed, was noted to again be involved in egg laying. Shortly after observations began, the snail's foot constricted (as in Figures 5 - 8) and an egg capsule appeared. The capsule was gently lifted out of the temporary egg groove as it was in transit from the gonopore to the ventral pedal gland. This capsule, not yet acted on by the pedal gland, was compared in gross morphology to an egg capsule laid immediately before by the same female.

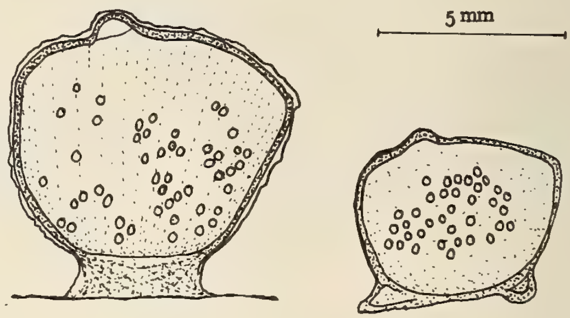

Figure 14

The egg capsule of *Melongena corona*.

A: a capsule fully acted on by the ventral pedal gland.

B: a capsule lifted from the temporary egg groove before it had entered the ventral pedal gland. Side view.

Figure 14 illustrates the difference in size of the 2 capsules. The pre-pedal gland capsule was very pliable and sticky. It was more or less amorphous and lacked any resilience. The post-pedal gland capsule was not sticky. It had a definite shape and would resume that shape after being folded or bent.

ACKNOWLEDGMENTS

We wish to thank Mr. Edward Hatfield and Mrs. Nelia López who were maintaining, for other purposes, the *Melongena corona* on which these observations were made. Mr. Marion K. Gray maintained the seawater system in which the specimens lived. Dr. Hilary B. Moore made helpful suggestions a: .d critically read the manuscript. This work was suppc.ted by Environmental Protection Agency Grant No. DI EPA WQO 18050 DMV.

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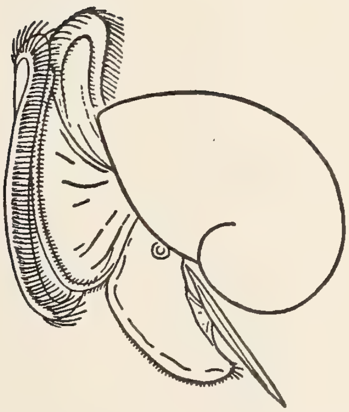

NOTES & NEWS

Some Nomenclatural Problems in Sacoglossa

BY

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PROBLEMS BEGIN WITH THE NAME to be adopted for this opisthobranch gastropod order. Priority would require Monostichoglossata or Stichoglossata Pagenstecher, 1874 (accepted by very few later authors); but priority does not apply to ranks higher than that of superfamily. In 1876 von Ihering proposed Sacoglossa and synonymized under it Bergh's manuscript name Ascoglossa. This action, as well as the two-to-one preference for Sacoglossa over Ascoglossa by subsequent authors, justifies continued usage of it.

The non-shelled sacoglossan forms have been grouped into a superfamily Elysiacea, based on the family Elysiidae and the genus *Elysia* Risso, 1818, oldest generic name in this complex. However, the family-group name Plakobranchidae Gray, 1840 (erroneously spelled Placobranchidae by him), has priority over Elysiidae H. & A. Adams, 1854; priority in family-group names is based on the date of proposal of the family, not on the oldest genus. Thus the superfamily name Plakobranchacea should replace Elysiacea – unless someone feels strongly enough that Elysiacea should be retained to submit a petition to the International Commission on Zoological Nomenclature for suspension of the Rules.

In the family Caliphyllidae, the genus *Polybranchia* Pease, 1860, is valid and not, as often assumed, preoccupied by Latreille, 1825, a usage that proves to be for a family-group taxon. The three replacement names *Lobifera* Pease, 1860, *Phyllobranchillus* Pruvot-Fol, 1933, and *Polyphylla* Pruvot-Fol, 1954 (an accidental misspelling that is doubly invalid by being preoccupied), are unnecessary.

The generic name *Hermaeina* Trinchese, 1874, in the family Hermaeidae falls as a synonym of the earlier *Aplysiopsis* Deshayes, 1864. The latter name must be accepted however inappropriate it may seem to be (surely no sacoglossan looks like an *Aplysia*!), for Deshayes' illustration of his type species is unmistakable. Another well-known generic name, *Placida* Trinchese, 1876, also falls as a synonym. The earlier taxon, *Laura* Trinchese, 1872, has been misunderstood. Although regularly cited in synonymy by authors, it was either considered a homonym of *Lauria* Gray, 1840, or a *nomen nudum* and given a wrong date. Trinchese in 1872 validly described *Laura* but without citing any species by name. He later described and assigned to *Laura* 3 species, one of which, *L. viridis* Trinchese, 1874, was designated as type by Thompson in 1973. A second, *L. tardy* Trinchese, 1874, is the type species of *Placida* and is congeneric.

The genus *Olea* Kjerschow-Agersborg, 1923, was described from the Puget Sound area. Because the radula is wholly absent in the adult, *Olea* was made type of a family, the Oleidae, by Thiele, 1931. Normally, the Sacoglossa are herbivorous, feeding on the sap of green algae, but *Olea* devours instead the egg masses of cephalaspidean opisthobranchs, as Sandra Crane has shown (The Veliger 14 (1): 57 - 59, July, 1971). Robert Burn, an opisthobranch specialist, suggests (*in litt.*) that *Olea* is not unique in this, for carnivorous habits have developed, at least sporadically, in certain other sacoglossans, all in the family Hermaeidae. As he points out, *Olea* is morphologically close to several genera in the Hermaeidae, differing mainly in that the radula is vestigial, and he advises that it should be ranked as a member of this family rather than in a family by itself.

The Ovulidae: Replacement Names for Four Ovulid Homonyms

BY

CRAWFORD N. CATE

IT IS REGRETTED that in a recent paper (CATE, 1973), there occurred four homonyms among 26 designated new generic names; their replacement is proposed herein. In order to avoid any more confusion in this matter than necessary, the stems of the replacement names will remain the same but with the addition of a suffix ending. They are as follows:

Galeravolva Cate, nom. nov.
(*Pro Galera* Cate, 1973. The Veliger 15 (Supplement): p. 5. Mollusca: Gastropoda, family Ovuli-

dae). (*non Galera* GRAY, 1842. Synopsis of the contents of the British Museum, ed. 44, pp. 12, 16. Mammalia [the name was also used by HERRE, 1927, Philippines Bureau of Sciences, Monograph **23**: 87, in Pisces]).

Cymbovula Cate, nom. nov.
(*Pro Cymbula* Cate, 1973. *ibid.*: p. 80). (*non Cymbula* H. & A. ADAMS, 1854. Genera of Recent Mollusca, vol. **1**: 466. Mollusca: Gastropoda, family Patellidae).

Hiatavolva Cate, nom. nov.
(*Pro Hiata* Cate, 1973. *ibid.*: p. 86) (*non Hiata* ZETEK & MCLEAN, 1936. The Nautilus **49**: 110. Mollusca: Pelecypoda, family Pholadidae)

Calcarovula Cate, nom. nov.
(*Pro Calcaria* Cate, 1973. *ibid.*: 106) (*non Calcaria* PORAT, 1878. Bih. Svenska Vetenskakad. Handlinger **4**: 7, 10. Phylum Arthropoda, Class Myriapoda).

I extend my sincere thanks to Dr. A. Myra Keen of Stanford University for help with the source material needed for this note.

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Subtidal Mussel Beds in Baja California with a New Record Size for *Mytilus californianus*

BY

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THE MOST CONSPICUOUS BIVALVE of the Pacific Coast of North America is the common California sea-mussel, *Mytilus californianus* Conrad, 1837. This species is typical of the intertidal zone of rocky coasts, although BERRY (1954) cited information from divers that living specimens had been observed at depths of 15 - 40 feet (4.5 - 12 m) off Palos Verdes, California. He also noted that a 228 mm specimen had been dredged from deep water off northern Humboldt County, California (Berry Coll. No. 17235).

In carrying on field work in Lower California I discovered aggregations of large *Mytilus californianus* on seamounts; the size of some of the individuals exceeds that of the largest individual recorded to date. These mussels have been observed on 2 field trips, one in July 1971 and the second in August 1972. The area investigated was the Roca Ben and Johnston seamounts, about 298 km south of San Diego, California and approximately 10 km west of Bahía de San Quentin, Baja California. The top of Roca Ben is about 10.5 m below the water surface, while the Johnston seamount is double peaked, with the higher peak at about 3 m depth and the lower peak at 18 m depth. The west side of both seamounts has a sheer face of about 12 m and old basalt flows can be observed. The mussel beds generally occupied the south and southeast sides of the seamounts ranging from the 24 m depth to the top of each pinnacle. The currents for the most part come from the northwest side of each peak, and in both years of observation, 1971 and 1972, the speed of the current was estimated to be about 8 knots (15 km) per hour on the tops of the seamounts. Thus, the mussel beds occupied the lee side of these seamounts.

The largest museum specimen of *Mytilus californianus* is Berry's 228 mm specimen noted above. The largest specimen I have measured is 251 mm long (Marin College collection A-1) from Johnston seamount. A second large specimen, collected from Roca Ben seamount, was 247 mm long and 111 mm wide. The wet weight of this specimen was 900 g. A 235 mm specimen was confirmed as *M. californianus* by the staff of the California Academy of Sciences in San Francisco (CASG collection Locality 47730). Interestingly, a bed of large mussels was also found intertidally on the south side of Punta Banda, near Ensenada, Baja California. The largest specimen noted there was 238 mm long (Marin College collection A-2). Additional specimens were collected from both seamounts and are presently in the Biology Museum of the College of Marin.

The mussel beds on the seamounts are characterized by the large sizes of the individuals present. At Roca Ben seamount a 1 m^2 quadrat was selected as a typical section of the large mussel beds; a total of 225 mussels were counted in this square. Ten of these mussels were pulled off randomly for examination; 6 were alive, the other 4 shells were empty. The average length of the 10 shells was 222 mm. The barnacle *Balanus tintinnabulum* (Linnaeus, 1758) was very abundant on these mussel shells; the mean number of barnacles on the 10 shells was 65.9. As well as the barnacles, numerous species of other organ-

isms were found growing on the 10 mussels, including 5 species of algae; 2 of sponges, 2 of hydroids, 4 of polychaetes, 2 of crustaceans, 3 of mollusks, and 6 of bryozoans. Among the larger mussels small individuals of 1 to 2 cm in length were noted, giving evidence of recruitment to the population. All in all, the mussel beds appear to be thriving and are dominated by large individuals.

The dominant seastar on the seamounts was *Pisaster giganteus* (Stimpson, 1857), some with arms spanning approximately 60 cm. All *P. giganteus* observed were on top of mussels. Twenty of these large seastars were pulled off to ascertain if they were feeding on the mussels; in all cases, however, they appeared to be feeding on the *Balanus tintinnabulum* attached to the mussels. No obvious predation on the large dominant mussels in the beds was observed.

Although some effort was made to obtain the largest specimen of *Mytilus californianus* in the populations on the seamounts, I suspect that still larger ones exist than those we did collect. A presumably larger specimen than is reported here was dropped on the way back to the boat after a long dive and regrettably time did not allow for more searching.

My profound appreciation to Dr. Cadet Hand, Director of the Bodega Marine Laboratory, University of California, is expressed for his assistance in my mussel studies.

Financial assistance was obtained from the Virginia Marine Resources and the National Marine Fisheries Service through the Commercial Fisheries and Development Act (88-309), Project No. 3-124-R.

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Many Thanks to the San Diego Shell Club

After the July issue of our Journal had gone to press, there arrived another generous donation to our Endowment Fund from the San Diego Shell Club. As the previous contributions, this latest gift will assist us in gradually attaining our goal, that of at least keeping the cost of our publication as low as possible and, eventually, to reduce membership dues — barring the effects of inflation.

ADDENDUM

Through an oversight the following statement was omitted in the manuscript of the paper by Loesch & Haven (see our July issue). It should be added on page 80 under "Acknowledgments."

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of $5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is $25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

Publication Date of THE VELIGER

The publication date of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Post Office does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

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Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

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to the fact that the office of the Manager has been moved to Florida — in February of 1972. The address is:

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INFORMATION DESK

A Source of Authors and Dates for Family Names of Gastropods

BY

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THE NECESSITY for observing priority in zoological family name usage (International Code of Zoological Nomenclature, 1964, Article 23 c, d; Article 36) has caused some diligent taxonomists to do a great deal of literature searching to discover the oldest family group name for a taxon. Since this is a comparatively new requirement, which some workers observe and some ignore – there is no orderly way to look up this information other than laboriously going over likely references in a hit or miss fashion.

For bivalves the problem has been solved with the publication of the "Treatise on Invertebrate Paleontology Part N, Mollusca 6 (1-3), (1969-1971)" as authors and dates of taxa above generic level are supplied. For gastropods, only a small percentage of the families has been completed in "Treatise, Part I, Mollusca 1 (1960)", covering some gastropods, chitons, scaphopods, and monoplacophorans. Some help is at hand at least for Recent families in the form of the French "Traité de Zoologie, Anatomie, Systématique, Biologie, vol. 5, Mollusques: Gastéropodes et Scaphopodes (Fascicule 3), Paris (1968)."

In the systematic section of this work by André Franc, and in the case of the scaphopods, co-author E. Fischer-Piette, authors and dates are supplied for taxa of ordinal rank and below, including superfamilies and families. One must search a bit for authors and dates of the classes and subclasses; however, they also are supplied at the beginnings of the appropriate sections. Franc gave no indication that I could find on the source of his data. In many cases data agree with those given in the complete "Treatise" sections on gastropods, but in a few cases differences are noted, possibly the result of independent research on Franc's part.

The information supplied in the "Traité" may serve as a starting point for the worker who is revising a group in his search for the earliest author of a family, and as a quotable reference for the more casual researcher who needs a rapid and probably credible source for this information. It should be noted that Drs. Franc and Fischer-Piette produced comparable works on the bivalved Mollusca, the Aplacophora and Polyplacophora, and H. Lemche and K. G. Wingstrand on the Monoplacophora in the "Traité" vol. 5 (fascicule 2), (1960), wherein similar data may be found, which, however largely have been superseded by the information in the cited "Treatise" volumes.

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Differentiation: The Meaning of ICZN Article 13 (a) (i)

BY

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HOW WIDELY AND CAREFULLY to compare a new species (or any other taxon) with other taxa is one of the more difficult decisions facing a potential author. The International Code of Zoological Nomenclature (STOLL, *et al.*, 1964) provides some guidance in this regard, but this guidance requires some explanation and interpretation.

The implications of ICZN Article 13 (a) (i) to authors wishing to propose new taxa, such as species or genera, are of great importance (MAYR, 1969). Unfortunately, this

rule has been given insufficient attention by malacologists, in part because it is subject to interpretation. It is the purpose of this note to put forward for **discussion** criteria which authors may wish to consider in meeting their obligations under this Article.

Article 13 (a) states that "a name published after 1930 must be either (i) accompanied by a statement that purports to give characters differentiating the taxon; or (ii) accompanied by a definite bibliographic reference to such a statement; or (iii) proposed expressly as a replacement for a preexisting name." Here we are mainly concerned with the first of these three alternatives, the other two options being less common derivatives.

What is "a statement that purports to give characters differentiating the taxon"?

It seems to me that in order to satisfy the requirements of ICZN Article 13 (a) (i) authors wishing to describe new taxa must generally go beyond a simple description. Their proposals must contain information explaining why they regard the taxon as new and which will help other workers to recognize the new taxon from among similar taxa. This information may be more or less detailed depending on present knowledge of the taxonomic group under study. It will generally be in the form of comparisons with other taxa, but this may not always be the case.

Some workers, in fact, hold that a detailed, exact, and properly illustrated description is by itself a sufficient basis for distinguishing a new taxon from other taxa. However, other workers feel that in contemporary malacology authors should make an effort to go beyond a mere description. For example, it would clearly be inappropriate to describe a "new, large pink murex" from the Panamic province without mention of the 3 species now recognized from that area, no matter how detailed the description of the new taxon.

Under this interpretation, "a statement that purports to give characters differentiating the taxon" is one by which colleagues can tell a new taxon from other, similar taxa. It is an important part of a description. It provides the proof that a taxon is to be regarded as new and the means by which others will be able to distinguish it from related or superficially similar taxa.

Most importantly, I think, Article 13 (a) (i) is to be viewed as a flexible rule requiring a flexible interpretation. The greater the number of taxa that exist in a group, the more similar they are to one another, and the better known the taxonomic group under study, the more detailed should be the "statement."

The following would seem to be desirable guidelines for authors and editors to adopt:

(1) Comparisons should be made, when appropriate, both with most closely related species and, if necessary, with any superficially similar species of the same geographic range that might cause confusion.

(2) The author should have examined other taxa sufficiently widely in space (geographically) and in time (geologically) to be reasonably certain that the taxon is new. This may be accomplished by a study of the literature or of actual specimens.

Evidence is accumulating that many molluscan species have survived for long periods of time and are distributed widely over the earth's surface. Sometimes distributions have changed significantly with time, even to the extent of species shifting from one ocean basin to another.

However, until there is equal development of malacology all over the world and until there are better means of information exchange and retrieval among systematists and museums, authors cannot be expected to compare, say, a Californian turbonillid with a species from East Africa. But an author should be familiar with all known west American species in the group under study at least as far back as the Pliocene.

Similarly, a knowledge of Caribbean species is essential if Panamic species are involved. Some familiarity with Indo-Pacific species is necessary if species from the Galápagos or Cocos Islands are being studied. If deepwater or pelagic species are under consideration, then the fauna of the entire world must be taken into account. If Arctic species are being investigated, an author should be familiar with the fauna of the entire Arctic, including its Pleistocene and Pliocene. Information about the fauna of Japan and Siberia is essential to a study of many northern Pacific groups.

(3) In well-studied groups like the Cypraeidae, Volutidae, Conidae, and Teredinidae, an author should have a reasonable knowledge of the entire family world-wide. In more poorly-known groups, such as the Turridae and Erycinidae, such comprehensive knowledge is, at the moment, neither necessary nor, perhaps, possible.

(4) There is no substitute for illustrations, diagrams, tables, or graphs. It is particularly desirable to illustrate both the new species and closely related or superficially similar species.

Four objections are often made to any such firm guidelines under Article 13 (a) (i). I think these objections can be met in part by these very guidelines.

It is said that if greater rigor is adopted, the availability of many taxa on the books would be brought into question. Under such guidelines, however, the past could just as well remain prologue, and the names of previously proposed taxa would continue to be available. This interpretation has to do with the future, not with the past.

It is said that a standard calling for comparison could cause some authors to make routine, meaningless compari-

sons simply to satisfy the standard. The objection is also made that comparisons will never completely satisfy other workers, or be regarded as adequate later in time. It seems to me that these two points are reasons for the best comparisons possible, not arguments against including any comparative information at all. The flexible interpretation here advocated is an effort to help authors make meaningful comparisons.

Finally, it is argued that some animals are so unique that comparison is impossible. This seems to be only a semantic problem. How does an author know that his animal is unique? – by comparison with other animals, but at a higher taxonomic level. Thus, proof that something is unique is equivalent to proof that it is not similar to other groups. Moreover, a flexible standard would require fewer specific comparisons for small, unique groups.

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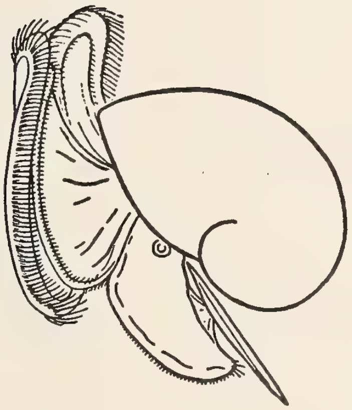
{Editor's note: The foregoing article is offered as a possible starting point for a debate, in this column, of the questions raised by Dr. Coan. Thoughtful replies, counter-arguments, and discussions will be welcomed and, if considered pertinent and contributing to a clarification of the admittedly involved problem, will be published in forthcoming issues of this journal.}



BOOKS, PERIODICALS, PAMPHLETS

Professor Kotora Hatai Memorial Volume

edited by Kiyoshi Asano, Nobu Kitamura, Tamio Kotaka, Yokichi Takayanagi, and Hisao Nakagawa. Tohoku University [Sendai, Japan] Science Reports, 2nd ser. (Geology), special volume no. 6 (Hatai Memorial Volume), 499 pp.; 57 plts. 1973

This impressive collection of 47 papers includes 30 reports on mollusks of the Pacific basin. Most of the reports deal with Tertiary and Holocene marine mollusks of Japan. Some pertain to the eastern North Pacific including reports on Miocene mollusks from the Alaska Peninsula (F. S. MacNeil), *Chlamys cosibensis* from the North Pacific margin (K. Masuda), North Pacific history of *Clinocardium nuttallii* (F. H. Kilmer), Tertiary Cassidids of western North America and Japan (S. Kanno), and marine Neogene molluscan research in North America (W. O. Addicott). There is also an excellent review of the sequence of Cenozoic molluscan faunas of southern Australia by N. H. Ludbrook. All but one of the papers on Cenozoic mollusks are in English.

Professor Hatai, the dean of Japanese molluscan paleontologists, retired in April 1973, from Tohoku University after a long and distinguished career summarized in dedicatory remarks by Tamio Kotaka. During his 40-year professional career, Hatai published approximately 300 papers, most of which are on Cenozoic mollusks.

WOA

Phylogenese, Adaptation und Migration einiger nordischen marinen Molluskengenera (*Neptunea, Panomya, Cyrtodaria* und *Mya*)

by Friedrich Strauch. Abhandl. d. Senckenbergischen Naturforschenden Gesellschaft no. 531; 211 pp.; 29 figs.; 11 plts. 15 November 1972

This comprehensive account of the biogeography and systematics of 4 circumpolar genera is a refreshing new appraisal of the interplay of paleogeography and climatic change upon the development of modern boreal and arctic molluscan faunas. Special emphasis is placed upon the latest Cenozoic history of these genera.

Opening of the Bering Straits during the late Cenozoic permitted migration of North Pacific genera via polar areas into the North Atlantic. Pacific taxa first appear in the Atlantic during the early Pleistocene; two or three waves of migration are recognized. Routes of migration are depicted on diagrams showing the fossil occurrence and distribution of modern populations of each genus.

Diagrams showing inferred phylogenetic relationships in each genus are indicative of accelerated evolutionary change during the late Pliocene and early Pleistocene associated with the cooling of polar areas.

There are sections on the taxonomy of each species including detailed treatment of both fossil and modern North Pacific species of *Neptunea, Panomya,* and *Mya,* each of which has a long Cenozoic history in the Pacific. Effective use of diagrams is made in advancing species concepts and biogeographic and phylogenetic inferences. Three new taxa of *Mya* and two each of *Neptunea* and *Panomya* are described. Most of the Pleistocene and Holocene species are illustrated. There is a useful compilation of references dealing with late Cenozoic boreal and arctic molluscan faunas.

WOA

Atlas of Monthly Mean Sea Surface and Subsurface Temperatures in the Gulf of California, Mexico

by Margaret K. Robinson. San Diego Society of Natural History, Memoir no. 5; 97 pp.; 87 figs. 16 April 1973

Mean monthly temperatures (in degrees Fahrenheit) for five levels (surface, 100, 200, 300, and 400 feet) are shown for the west coast of Mexico from Cabo Corrientes (lat. 20° N) to Ensenada (lat. 32° N). The striking temperature contrast between the Gulf of California and the Pacific coast of Baja California and the occurrence of upwelling along both the Mexican and Baja California Coasts are evident from these charts.

The surface and 100-foot charts should be of interest to malacologists and biogeographers as frames of reference for analyzing the distribution of taxa from the Californian, Surian, and northern Panamic molluscan provinces.

WOA

Mollusc Fauna of the Hungarian Upper Oligocene (Egerian), Studies in Stratigraphy, Palaeoecology, Palaeogeography and Systematics

by Tamás Báldi. Akadémiai Kiadó, Budapest, Hungary, 511 pp.; 55 figs.; 51 plts.; $19.50 from Kultura, Bulapest 62, P. O. Box 149. 1973

The shallow-water molluscan fauna of the late Oligocene Egerian Stage (about 25 to 31 million years old) consists of 240 gastropod and pelecypod taxa. Báldi has developed an unusually thorough synthesis of the paleontology and geology of this central European unit. The Egerian mollusks are exceptionally well preserved; original coloration

is preserved on several gastropods. The fauna is subdivided to 14 littoral and sublittoral communities all but 4 of which represent depths of less than 30 meters. Excellent sections on European stage-age correlation and on the Oligocene/Miocene boundary are included.

This well-illustrated, definitive treatment of the late Oligocene of Hungary should be of special interest to Tertiary paleontologists since it includes warm-water Mediterranean elements in addition to boreal elements in common with the type late Oligocene of Northern Germany.

WOA

Bibliography and Zoological Taxa of Paul Bartsch

by Florence A. Ruhoff. Smithsonian Contributions to Zoology - No. 143; 166 pp. For sale ($2.85 domestic postpaid) by Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402. 20 July 1973

This is a very valuable addition to the working library of any serious taxonomist since Paul Bartsch, in a long and highly productive life, established a grand total of 3 278 molluscan taxa. This new work is a welcome companion to the earlier lists concerned with the work of Dall, Pilsbry, and Gould. The format is the same as in these other lists, that is, a complete bibliography is followed by an alphabetical enumeration of the taxa; in addition to the names information about each taxon includes type locality; original generic assignment; type number; as well as a concise bibliographic citation of the original description. In view of today's printing costs, the price is extremely low and Dr. Ruhoff is to be thanked for this painstaking work.

RS

Polyplacophora of the Caribbean Region

by P. Kaas. Studies on the Fauna of Curaçao and other Caribbean Islands, vol. 41, pp. 1 - 162; 247 text figs.; 9 plts.; 2 tables. Martinus Nijhoff, The Hague, 1972

The chiton fauna of the Caribbean is associated with the names of many famous early malacologists: Linnaeus, Chemnitz, Gray, Broderip, the first two Sowerbys, Reeve, the Rev. Lansdowne Guilding, C. B. Adams, Shuttleworth, Dall, and Pilsbry, to mention some of the better known. As the literature on Caribbean chitons is scattered widely, and as the knowledge of many named species is sparse, Dr. Kaas has done a great service by bringing together past as well as current information on species described from the region. The latter is based largely on a collection of 1500 specimens made by Dr. P. Wagenaar Hummelinck between 1936 and 1967, covering 21 species, of which 4 are described as new.

Dr. Kaas is a fine systematist and his treatment is complete, even including keys to families, genera and subgenera. Discussion of each species covers detailed synonymies, occurrences on the various Caribbean islands, up-to-date descriptions, and comments on individual species variations. There is a good index and the bibliography of 145 titles seems quite complete.

A major feature of the report is the large number of excellent line drawings of chiton valves and enlarged renditions of girdle scales and other girdle ornamentations. The plates are made up of unusually clear photographs, many of them enlarged, both of whole animals and of disarticulated valves. No student of chitons, be he amateur or professional, should have difficulty identifying Caribbean species with Dr. Kaas' comprehensive work at hand.

AGS

The Mollusks of the Arid Southwest with an Arizona Check List

by Joseph C. Bequaert & Walter B. Miller. The University of Arizona Press, Tucson, Arizona. xvi + 269 pp.; 6 text figs. $8.-. 1973

While the molluscan fauna of the desert areas of the southwestern United States has received considerable attention in recent years, nowhere has its character and composition been brought together under a single title until now. The region long has been known for its interesting and varied land-snail genera including *Ashmunella, Holospira, Humboldtiana, Oreohelix,* and *Sonorella,* each with a number of localized species and races. Thus, it is appropriate that the first part of this study be devoted to an excellent discussion of the zoogeography of southwestern nearctic mollusks.

Part II of the study consists of a check-list of Recent land and freshwater Mollusca of Arizona with detailed accounts of the known occurrences of each species and with the taxonomy brought up-to-date. The list covers a total of 173 valid species and 46 recognized subspecies (140 land and 33 freshwater), of which 155 are native (128 land and 27 freshwater). Introduced species are 18 in number (12 land and 6 freshwater). As might be expected, the helminthoglyptid genus *Sonorella* is represented best with 68 species and 18 recognized subspecies.

Both authors are experienced malacologists. Dr. Bequaert is well known for his many contributions to a general knowledge of the land and freshwater mollusks; Dr. Miller contributes much as the result of recent intensive field work in the area. The thoroughness devoted to the study is indicated by the comprehensive bibliography of 570 titles following the check-list.

Students of the fauna and flora of desert regions will find Bequaert & Miller, 1973, an important and indispensable reference. Some may regret the lack of illustrations, but in most instances good, modern figures of the listed species already are available in published works, references to them being covered both in the narrative and the bibliography.

AGS

Tertiary Marine Mollusks of Alaska: An Annotated Bibliography

by Warren O. Addicott. Geological Survey Bulletin 1343: 30 pp.; 3 text figs. For sale: Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402. Price 25 cents. 1971

In this short publication a concise summarizing annotation is given for 135 papers dealing with the subject matter indicated by the title of the present article.

RS

Fossil Chitons from the Mesozoic - A Checklist and Bibliography

by Allyn G. Smith. Occasional Papers of the California Academy of Sciences no. 103; 30 pp. 27 April 1973

This publication is the result of an exhaustive review of the literature relating to fossil chitons. There is a revision of systematic assignments,; a systematic arrangement is given next; and the annotated check list, occupying the major portion of the pamphlet, is followed by a bibliography of 28 titles.

RS

The Shore Fishes of Hawaii

by David Starr Jordan & Barton Warren Evermann. Charles E. Tuttle Company, Rutland, Vermont 05701. 392 pp.; 229 text figs.; 16 plts. in color, and 16 in B & W. $8.50. 24 August 1973

While fishes as such are not the subjects for study by malacologists, we do think, however, that this re-issue of a classic might be of interest to the many snorkeling and SCUBA-diving shell collectors, since they may well meet some of these so-to-speak face-to-face-plate. The cost, in view of today's printing charges, is moderate enough. The original work, published in 1903, included 83 color plates, each portraying one species of fish; in this book, material economies have been achieved by combining 4 or more of these original plates into a single plate. The same was also done with the black-and-white plates, of which 65 have been combined into 16. Modern printing methods, however, are so much improved that these reproductions leave little to be desired.

Both authors were the foremost authorities in their time; Jordan was professor at Stanford University and Evermann, for many years, was the Director of the California Academy of Sciences. Their work was THE standard work for many years and it still is to be considered a classic, although taxonomic progress has necessitated many nomenclatural changes which are not reflected in this re-issue. And even though the book's title indicates Hawaii as the home of these fishes, many, if not most, of them do occur in various parts of the Pacific area. A shell collector will have a friendly feeling toward the playful and curious finny creatures that he encounters if he is acquainted with their species. And this book will certainly make such an acquaintance possible.

RS

Sharks & Rays

by Spencer Wilkie Tinker & Charles J. DeLuca. Charles E. Tuttle Company, Rutland, Vermont 05701. 80 pp.; 44 text figs. $7.25. 27 July 1973

Since sharks are known to be dangerous to man - at least some shark species - it is a wise shell collector who makes an effort to know these creatures who might attack him; it is also worth while to know which species are not a danger to man, so that unnecessary anxieties can be avoided. Since the various species treated in this book are encountered in warm waters, the information may be valuable not only to collectors in Hawaii, but in many other areas rich in mollusks.

RS

Evidence for the Origin of the Mactridae (Bivalvia) in the Cretaceous

by Louella R. Saul. University of California Publications in Geological Sciences, vol. 97; 63 pp.; 3 plts.; 8 text figs.; 1 table. $4.-. 14 February 1973

Two new genera, one new subgenus and 5 new species are described. Convincing arguments, elegantly presented, support the thesis of the author.

RS

Cephalopoda from the Eastern Mediterranean

by G. Ruby & J. Knudsen. Israel Journal of Zoology, vol. 21, pp. 83 - 97; 2 plts.; 1 text fig. 1972

This brief but well organized paper is based on a collection of 189 specimens, comprising 17 species. The problem of trans-Suez-Canal migration of some species is considered.

RS

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

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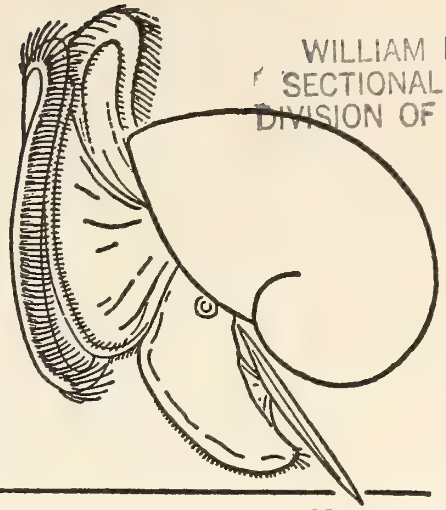
A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

THE VELIGER



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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, *(Subgenus)*
New Taxa

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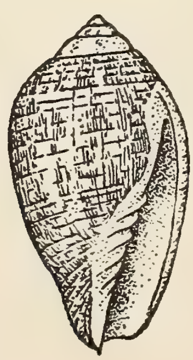

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Zoogeographic Significance of a Late Quaternary Occurrence of the Bivalve *Astarte* off the Central California Coast [1]

BY

WARREN O. ADDICOTT

U. S. Geological Survey, Menlo Park, CA 94025 and Stanford University

AND

H. GARY GREENE

U. S. Geological Survey, Menlo Park, CA 94025

(1 Plate; 1 Map)

INTRODUCTION

Abundant fossil specimens of a small, high-beaked *Astarte* dredged off the central California coast (lat. 36° 27′N) constitute a unique southward range extension of this cool-water genus in the eastern North Pacific during what is believed to be the latest Pleistocene time. Today the genus *Astarte* ranges southward along the eastern North Pacific coast to the Strait of Juan de Fuca (lat. 48° N), where it is represented by several living species. Its southernmost previously known occurrence during the late Pleistocene was in the nearby Strait of Georgia area (lat. 49°30′N) of southernmost British Columbia (Wagner, 1959). The new record of this cool-water genus off central California is inferred to represent a brief but significant southward extension of range during the Wisconsin Glaciation and this is taken as evidence of cooling of the shallow-water environment.

OCCURRENCE

Some 60 specimens of *Astarte loxia* Dall, 1903 were recovered from a dredge haul made by Greene on November 5, 1971 near the head of an unnamed tributary to Monterey Submarine Canyon about midway between the mouth of Carmel River and Point Sur and about 5 km offshore (Figure 1). The dredge started at lat. 36°26′N and long. 122° W and terminated at lat. 36°27′30″N and long. 122° 01′W. Over this course the dredge hit bottom at a depth of 300 m. Dredging continued upslope to a depth of 180 m. The dredge, an 18- by 36-inch (45 by 90 cm) pipe dredge,

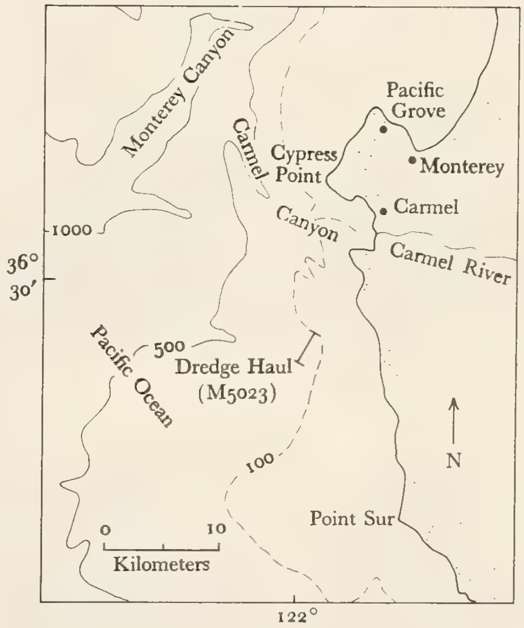


Figure 1

Index map showing location of dredge haul (USGS Cenozoic loc. M5023). Bathymetric contours in fathoms.

[1] Publication authorized by the Director, U. S. Geological Survey

yielded well-sorted, medium- to coarse-grained unconsolidated sand containing pebbles of granite, chert, and shale and abundant shells. Living mollusks and other larger invertebrates were separated from the sample. The fossiliferous component has been assigned USGS Cenozoic locality no. M5023.

PALEONTOLOGY

The small specimens of *Astarte loxia* Dall (Figures *6* to *9*) are exceptionally variable in shell outline. They are characterized by an accentuated, anteriorly pointed beak, and by a rounded ventral margin. Most are highly inequilateral in outline (Figures *6* to *9*). The surface is nearly smooth, being marked only by very fine concentric growth lines. There is no tendency for these lines to be accentuated in the umbonal region as on certain weakly sculptured forms of the similar North Atlantic and North Pacific species *A. montagui* (Ockleman, 1958: 84; MacGinitie, 1959: 168).

Dall (1903: 943) described *Astarte loxia* as a "pale oblique variety" of *A. rollandi* Bernardi based upon material dredged from 20 fathoms (36m) off the Semidi Islands about 175 km southwest of Kodiak Island, Alaska. This previously unfigured taxon is here considered sufficiently distinct from the large, thick-shelled *A. rollandi* to be treated as a full species. Specimens in the type lot are characterized by a variable outline, a produced posterior extremity, an accentuated beak, a heavy hinge with a swollen area extending from beneath the cardinal area to the deeply sunken anterior muscle scar, and a smooth exterior marked only with fine, irregular lines of growth (Figures *2* to *5*). *Astarte loxia* ranges from Akutan Pass in the Aleutian Islands (long. 166° W) northeastward to Prince William Sound, Alaska (Burch, 1944 (39): 6). Although characteristic of the North Pacific rim, the species has been dredged off the outer coast of northwestern Washington near Destruction Island (Figures *12*, *13*) and there is a doubtful occurrence from the nearby Straits of Juan de Fuca, Washington (USNM 222364). *Astarte loxia* is an inner sublittoral species in the northern part of its range, occurring in sand and gravel at depths of 12 to 34 fathoms (21.6 to 61.2m); off Washington, however, it ranges into the outer sublittoral zone having been dredged from between 50 and 100 fathoms (90 and 180m) near Destruction Island.

Astarte loxia is similar to *A. bennetti* Dall, 1903, a species that seems to have been incorrectly identified by many workers because the holotype (Figures *14* to *17*) has not previously been illustrated and the original illustration used by Dall (1903: plt. 63, fig. 6) in describing this species was a specimen from the Bering Sea (USNM 109279) that differs significantly from Dall's holotype from the Arctic Ocean (USNM 83221). As might be expected, subsequent recognition of *A. bennetti* (MacNeil, 1957: plt. 15, figs, 10, 11; plt. 16, fig. 10; Habe, 1964: plt. 55, fig. 7) seems to have been based upon the illustration of the specimen from the Bering Sea and not on the unfigured holotype.

The holotype of *Astarte bennetti* (USNM 83221) differs significantly in outline from Dall's Bering Sea specimen. It is a smooth, elongate individual with a straight growth line segment along the posterior ventral margin and an acutely rounded posterior extremity (Figures *14* to *17*). In contrast, Dall's (1903: plt. 63, fig. 6) illustrated specimen from the Bering Sea has regularly rounded ventral and posterior margins but differs from the type, and from *A. loxia*, in having fine concentric ribbing on the posterior one-third of the valve. The ribbing is not clearly

Explanation of Figures *2* to *17*

(all figures × 3 unless otherwise noted)

Figure *2*: *Astarte loxia* Dall, **paralectoype**, USNM 647234, sta. 1152 Semidi Islands, Alaska. Holocene. × 2½

Figure *3*: *Astarte loxia* Dall, **paralectotype**, USNM 647235, sta. 1152 Semidi Islands, Alaska. Holocene. × 2½

Figures *4* and *5*: *Astarte loxia* Dall, **lectotype**, USNM 169531, sta. 1152 Semidi Islands, Alaska. Holocene × 2½

Figures *6* and *7*: *Astarte loxia* Dall, USNM 647236, USGS Cenozoic loc. M5023, dredged off central California near lat. 36°18′N and long. 122°W. Late Pleistocene.

Figure *8*: *Astarte loxia* Dall, USNM 647237, USGS Cenozoic loc. M5023, dredged off central California near lat. 36°18′N and long. 122° W. Late Pleistocene.

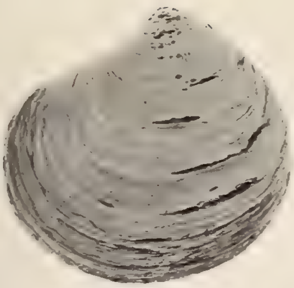
Figure *9*: *Astarte loxia* Dall, USNM 647238, USGS Cenozoic loc. M5023, dredged off central California near lat. 36°18′N and long. 122° W. Late Pleistocene.

Figure *10*: *Astarte* cf. *A. arctica* Gray, SUPTC 10071, Stanford Univ. loc. 41721, Work Canal, British Columbia. Holocene. × 2½

Figure *11*: *Astarte* cf. *A. arctica* Gray, SUPTC 10072, Stanford Univ. loc. 41721, Work Canal, British Columbia. Holocene. × 2½

Figures *12* and *13*: *Astarte loxia* Dall, CAS 53662, California Acad. Sci. loc. 39500, near Destruction Island, Washington. Holocene.

Figures *14* to *17*: *Astarte bennetti* Dall, holotype, USNM 83221, Bennett Island, Arctic Ocean. Holocene.



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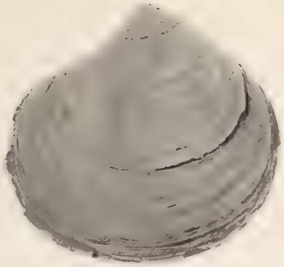

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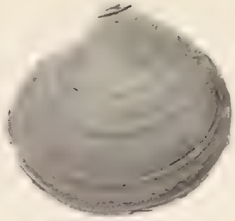

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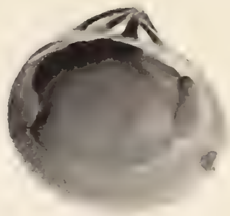

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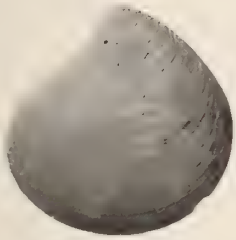

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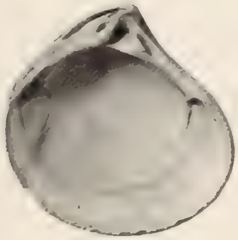

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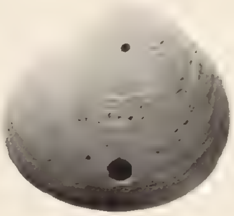

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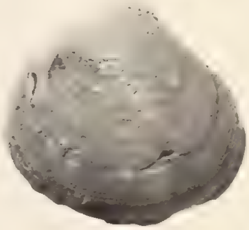

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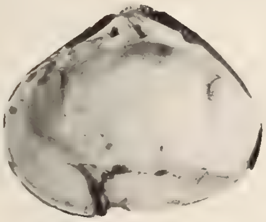

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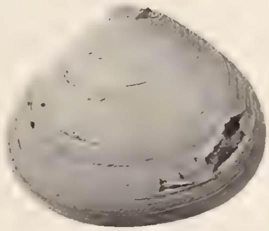

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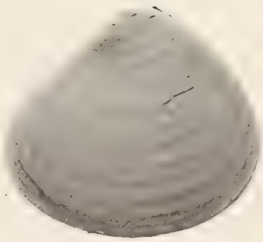

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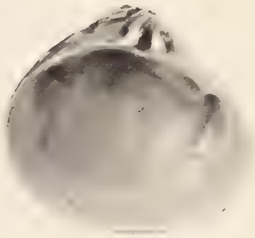

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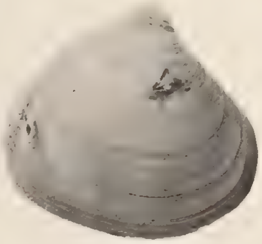

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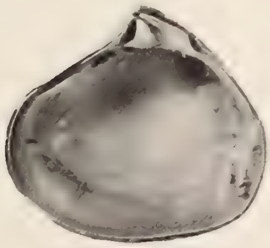

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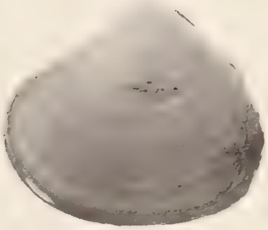

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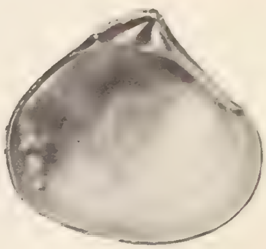

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depicted on DALL's (1903: plt. 63, fig. 6) figure, a line drawing. It seems likely that the holotype of *A. bennetti* is a different taxon than all other material illustrated as that species owing to this confusion and it seems possible that some of the identifications of *A. bennetti* may, in fact, be of the smooth-shelled *A. loxia*.

The small specimens of *Astarte loxia* from central California appear to be closely related to, if not conspecific with, a suite of smooth specimens with an exceptionally variable outline from the Chukotsk Peninsula, Russia. These specimens, identified as *A. montagui* (Dillwyn) by PETROV (1966: 210-211; plt. 15, figs. 8-15), are from glacio-marine deposits of early or late Pleistocene age. The somewhat elongate, inequilateral outline and smooth exterior of the Chukotsk specimens invite comparison with *A. loxia* and also with Quaternary specimens of *A. bennetti* from the Gubik Formation of Arctic Alaska figured by MACNEIL (1957). They appear to lack the concentric undulations characteristic of the umbonal area, and frequently the entire shell, of *A. montagui*.

AGE

All taxa of this assemblage are still living so far as can be determined. The genus *Astarte*, however, is locally extinct; today it occurs no farther south than the Puget Sound area of northwestern Washington. Other extralimital northern mollusks occur in late Pleistocene assemblages from the lowest marine terrace of the nearby Santa Cruz Mountains (ADDICOTT, 1966). These older, cool-water assemblages have been radiometrically dated at between about 70000 and 100000 years (BRADLEY & ADDICOTT, 1968).

A comparable late Pleistocene range extension of the northern sea cow *Hydrodamalis gigas* Zimmermann (JONES, 1967) may have some bearing on the age of the *Astarte* association from loc. M5023. A fragment of the skull of this extinct marine mammal was recovered by a trawler from shallow water between Point Sur (Figure 1) and Santa Cruz, California. This species once lived in the Commander Islands of the southwestern part of the Bering Sea (lat. 55° N). Carbon-14 analysis of the specimen provided an age of about 19000 years B. P. (JONES, 1967), indicating that cold-water marine mammals extended their range southward into the middle latitudes of the eastern North Pacific at or near the peak of the Wisconsin Glaciation. In view of the bathymetric setting of the larger invertebrate assemblage and the somewhat comparable southward extensions of *Astarte* and of *Hydrodamalis*, it can be postulated that the assemblage from loc. M5023 is of latest Pleistocene age and may approximate the 15000- to 19000-year troughs on MILLIMAN & EMERY's (1968: 1122) sea level curves.

ZOOGEOGRAPHIC SIGNIFICANCE

The occurrence of *Astarte* off central California represents a significant geographic range extension in terms of its previously known late Cenozoic occurrences along the Pacific coast. *Astarte* is a cool- to cold-water genus according to its modern distribution along the eastern North Pacific margin. Its southernmost modern occurrence is in the Puget Sound area (lat. 48°), where it is represented by 7 species (Table 1). This range limit is coincident with an important faunal province boundary that marks the southern outpost of many other cool-water mollusks (VALENTINE, 1966: fig. 3). North Pacific molluscan assemblages north of latitude 48° N are commonly referred to the Aleutian molluscan province (SCHENCK & KEEN, 1936; HALL, 1964; and COAN, 1971).

The occurrence of *Astarte loxia* off northwestern Washington is a significant southeastward range extension of this species from previously known occurrences near the head of the Gulf of Alaska. All of the previously reported species from the Puget Sound area excepting *A. arctica* Gray (RICE, 1971: plt. 31, fig. 198) are distinct from *A. loxia* in having prominent concentric ribbing on the umbonal region and on most of these this pattern extends to the ventral margin. The smooth specimen figured by RICE (1971) as *A. arctica* differs from specimens of *A. loxia* in having an elongate shell with non-accentuated beaks. These differences are illustrated by specimens from southwestern British Columbia (Figures *10, 11*) that seem to be conspecific with RICE's (1971) *A. arctica*.

Table 1

Species of *Astarte* reported
to be living in the Puget Sound-Strait of Georgia area
(lat. 48° - 49° N)

Astarte alaskensis Dall	BURCH (1944, no. 39: 6)
Astarte arctica Gray	RICE (1971: 77)
Astarte compacta Carpenter	BURCH (1944, no. 39: 6)
Astarte esquimalti Baird	BURCH, (1944, no. 39: 7)
Astarte loxia Dall	This report (CAS loc. 39500)
Astarte montagui (Dillwyn)	MACGINITIE (1959: 169)
Astarte willetti Dall	BURCH (1944, no. 39: 6)

It is of interest that the southernmost previously known late Quaternary and Holocene fossil records of *Astarte* also are from the Puget Sound-Strait of Georgia area near lat. 49° N. All are of the concentrically ribbed species *A. alaskensis* Dall, 1903, which has been reported from latest Pleistocene and Holocene deposits in southwestern British Columbia (Johnston, 1923; Crickmay, 1929; Wagner, 1959) and from Holocene glacio-marine drift in northwesternmost Washington (Easterbrook, 1963). A cool-water element composed of species now restricted to the Aleutian molluscan province is characteristic of late Pleistocene assemblages from marine terraces exposed along the Oregon and California coasts to the south (Addicott, 1964, 1966; Zullo, 1969), but the genus *Astarte* has never been found in any of these. So far as is known, these are the earliest fossil occurrences of this genus southeast of the Gulf of Alaska where *Astarte* has been recorded from the Yakataga Formation (Miller, 1957) in strata believed to be of late Miocene age (Durham & MacNeil, 1967).

The apparently brief range extension of the genus *Astarte* from the Puget Sound area to central California during the late Quaternary, a distance of some 1 500 km, is taken as evidence of climatic cooling associated with Wisconsin Glaciation. This postulate is strengthened by the occurrence of a 19 000-year-old specimen of the extinct northern sea cow *Hydrodamalis gigas* in a comparable depositional setting off this part of the central California coast.

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Some Comments on *Lobiger souverbii* Fischer, 1856, Re-Identified, of Japan

(Opisthobranchia : Sacoglossa : Lobigeridae)

BY

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(3 Text figures)

In 1952, I established *Lobiger sagamiensis* based on a single specimen collected by the Biological Laboratory, Imperial Household, from Sagami Bay, Japan. It appeared to me that this species differed locally from the Indian form, *L. nevilli* Pilsbry, 1896, in the possession of denticulations (striations) which, while existing in the latter on the teeth in the ascus, were found to occur in the former on those in the descending series of the radula. Subsequently 3 additional specimens from the same locality were offered to me by the Biological Laboratory for a continued study of the species. These arrived in a preserved state.

In 1971 I had a chance to keep and observe in my laboratory living material of *Lobiger* brought back by Dr. T. Yamasu from Amami Ohshima Island in the southern Sea of Japan.

Moreover, I was allowed to refer to some coloured sketches of *Lobiger*, prepared in 1971 by Mr. I. Hamatani from 3 living specimens collected by him from Cape Shiono-misaki in the province of Kii, Middle Japan.

All 8 specimens before me appear to belong to the same species, *Lobiger sagamiensis* Baba, 1952, which, in turn, becomes necessary to be revised in the light of later information concerning the taxonomy of the genus *Lobiger* presented by different authors (see Marcus, 1957; Gonor, 1961; Kay, 1964; Burn, 1966; and Marcus & Marcus, 1967).

The purpose of the present paper is to present some supplemenatry notes to my previous description. *Lobiger sagamiensis* Baba, 1952 is here referred to the West Indian species, *L. souverbii* Fischer, 1856, primarily due to the discussion by Kay, 1964.

Lobiger souverbii Fischer, 1856

(Japanese name: Furisode-Midorigai)

(Figures 1 to 3)

Main synonymy:

Lobiger souverbiei. Marcus, 1957: 398 - 402; figs. 17 - 29. - Santos (Brazil). Marcus & Marcus, 1963: 16. - Curaçao (West Indies). Marcus & Marcus, 1967: 25 - 27. - Biscayne Bay (Florida). Kay, 1964: 193 - 194; plt. 9, fig. 3. - Hawaii. Sphon & Mulliner, 1972: 150. - Galápagos Islands.

Lobiger souverbii. Sphon, 1971: 369. - Santa Cruz (Mexico).

Lobiger nevilli. Eliot, 1906: 307 - 310; figs. 3 - 4. - Chuaka (Zanzibar) and S. India.

Lobiger sagamiensis Baba, 1952: 337 - 338; figs. 1 - 3. - Sagami Bay. Baba, 1955: 8 - 9, 40; plt. 2, fig. 6, text figs. 6, 7. - Sagami Bay. Baba, 1961: 62; plt. 4, fig. 7. - Sagami Bay.

Distribution: Indian Ocean (Zanzibar; South India); Pacific Ocean (Japan; Hawaii; Galápagos Islands; Mexico); and Atlantic Ocean (West Indies, the type locality; Florida; Brazil).

Material referred to in this paper:

1 One specimen in the collection of Dr. T. Yamasu from *Caulerpa racemosa* in Amami Ohshima Island of Southern Kyushu, Japan, June 9, 1971 (main material for the following description).

2 Three specimens in the collection of the Biological Laboratory, Imperial Household, from *Caulerpa brachypus* in Misaki, Sagami Bay of the upper part of Middle Japan, August 24, 1951.

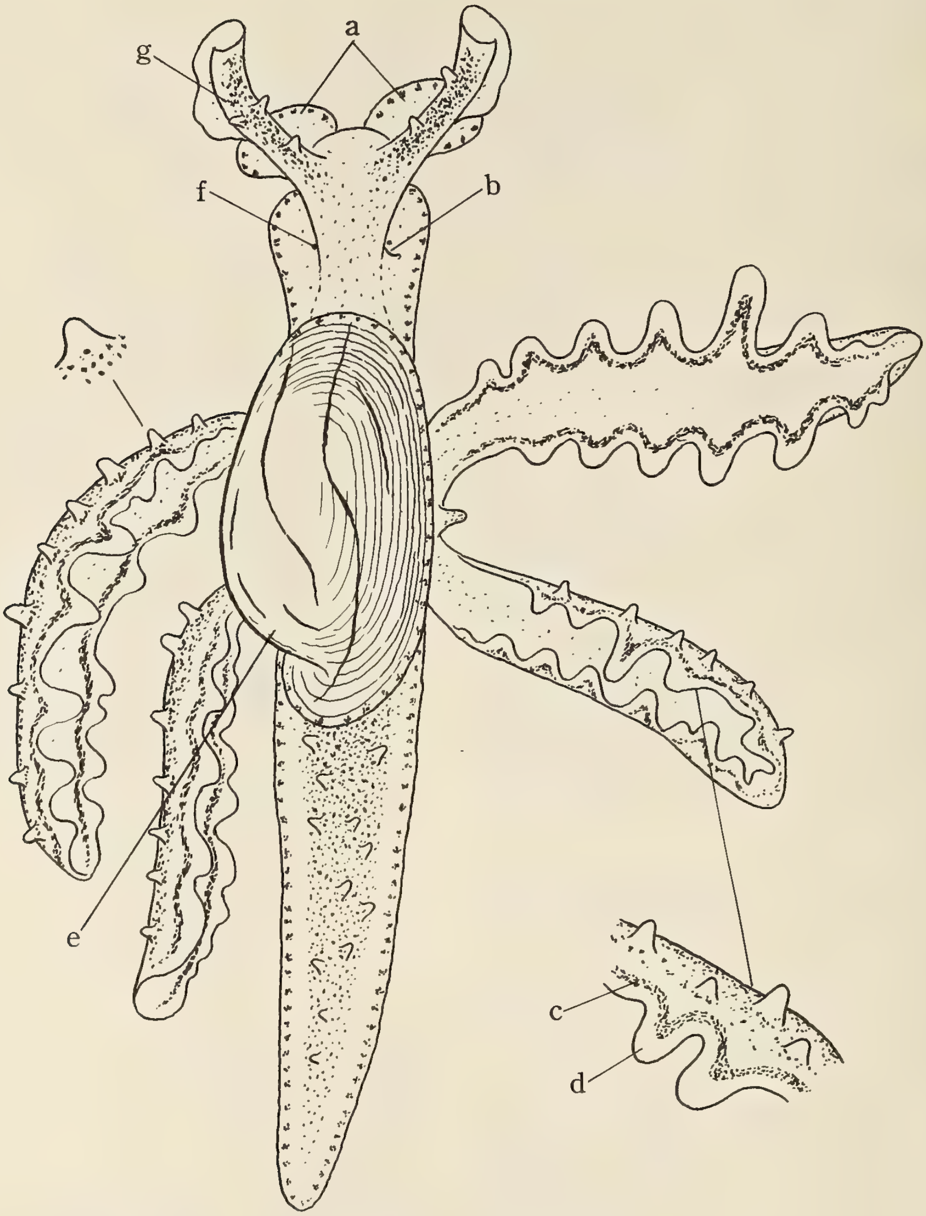

Figure 1

Lobiger souverbii Fischer, 1856
from Amami Ohshima Island, Japan

Living animal from dorsal side, length 15 mm

a – oral lobe b – male orifice c – vermilion red band
d – whitish border e – umbo with a concealed protoconch
f – eye g – rhinophore

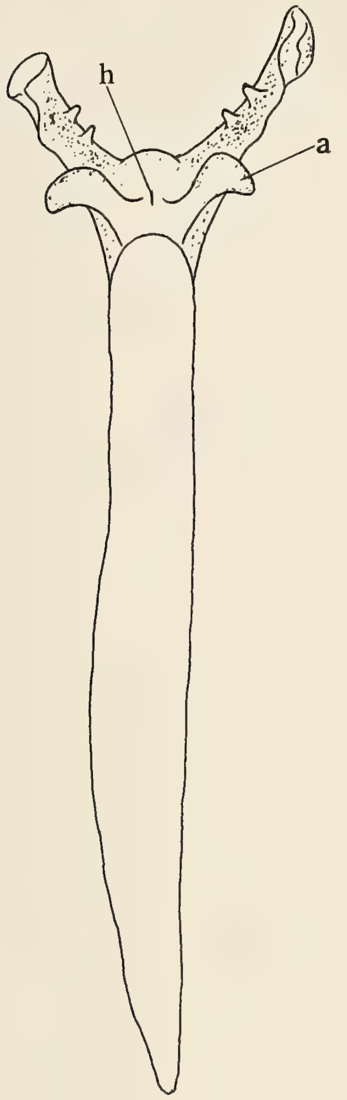

Figure 2

Lobiger souverbii Fischer, 1856
from Amami Ohshima Island, Japan

The same animal, ventral view

a – oral lobe h – mouth

3 Three specimens in the collection of Mr. I. Hamatani from *Caulerpa brachypus* at Cape Shiono-misaki of the lower part of Middle Japan, March 28, 1971.

Description: Total length of the animal in a crawling position is about 15 mm. The external configuration of the body is shown in the accompanying figures.

The parapodial lobes which stand normally over the shell are, as usual, deeply crenulated on their margin. There are bluntly conical tubercles scattered on the lower (= outer) surface of the parapodia, on the tail and sometimes on the rhinophores. The head is provided with paired oral lobes and paired rhinophores which are typically auriculated. The foot may be expanded flat.

The general ground colour of the body above is a faintly yellowish green, and there are chocolate-brown spots and opaque white dots, both of which are distributed rather densely over the head, rhinophores, median part of the tail and lower surface of the parapodial lobes. The margin of the oral lobes, foot and mantle is spotted with chocolate-brown. The tubercles on various structures are whitish to yellowish. The rhinophores are inclined to be yellow to the tip. The upper (= inner) surface of the parapodial lobes and the sole are uniformly pale yellowish green. A longitudinal black line was not noticed on the side of the head and neck of the present animal. On the mantle, however, there occurs a number (about 8) of mostly longitudinally running, bluish black streaks which are either simple or form some thickenings in the middle of their length. These streaks may show each a silvery lustre through the colourless transparent shell overlying the mantle. The crenulated margin of the parapodial lobes is marked with a vermilion red band just inside the whitish border.

The radula contains 6 teeth in the ascending series, 8 in the descending series, and about 12 in the ascus. The teeth are colorless. On each tooth there is an apical notch which is usually accompanied by a narrower one immediately above it (similar notches were noted to occur also in the type of *Lobiger sagamiensis,* the radular preparation of which is being re-examined presently). As for the teeth in the ascus, they are each possessed (as found recently from the type of said species) of a series of fine denticulations on either side of the cusp.

DISCUSSION

1. It is assumed here that *Lobiger sagamiensis* Baba, 1952 of Japan is referable to *L. souverbii* Fischer, 1856

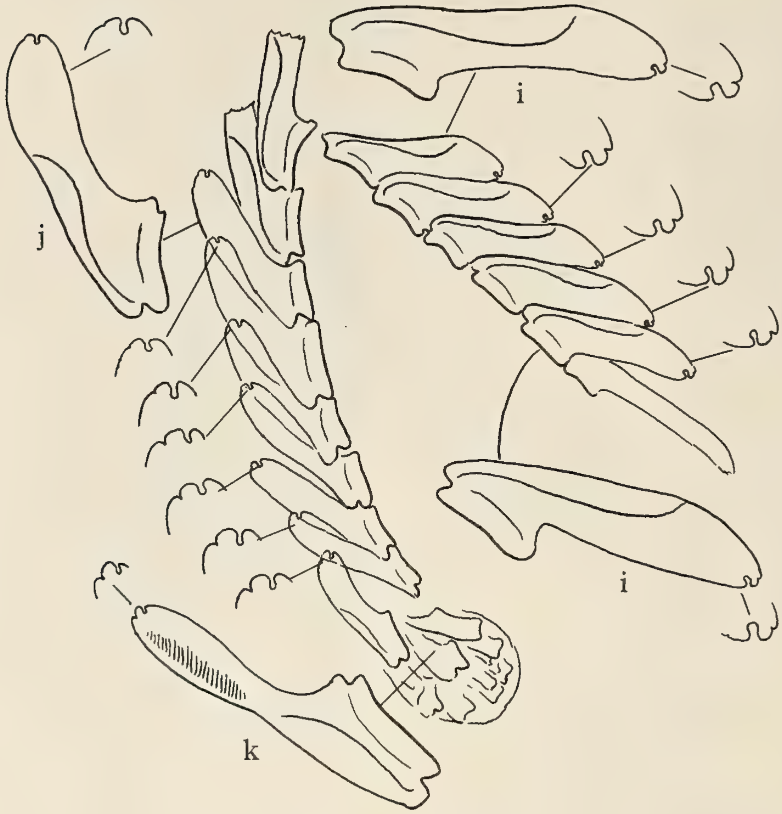

Figure 3

Lobiger souverbii Fischer, 1856
from Amami Ohshima Island, Japan

Entire radular ribbon from left side × 35
i – teeth in the ascending series × 75
j – a tooth in the descending series × 75
k – a tooth in the ascus × 150

from the West Indies and vicinity; the main points of agreement of the two are (1) the general form of the body, (2) the yellowish green colour of the body which is marked with a number of bluish black streaks on the mantle and with an orange red band on the border of the parapodial lobes, (3) the presence of notched cusps on all the radular teeth, and (4) the possession of lateral denticulations which are to be found on the oldest teeth laid down in the ascus.

2. For most of the same reasons stated above, *Lobiger nevilli* Pilsbry, 1896 from the Indian Ocean and *L. souverbii* of KAY, 1964 from Hawaii are also referable to *L. souverbii* of the West Indies.

3. *Lobiger viridis* Pease, 1863 from the Fiji Islands is stated by BURN (1966) to be different from other species of the genus in a number of anatomical details (the distinctly triganglionated visceral loop, the non-denticulated smooth teeth of the radula which show a notched cusp on the last 3 only in the descending series, the more or less short and thick crop, and the laterally ribbed diverticulum of the oesophagus). In colour patterns of the body, however, this species is almost akin to *L. souverbii* Fischer from various seas.

4. Apparently *Lobiger serradifalci* (Calcara, 1840) from the Mediterranean is most clearly associated with *L. souverbii,* as stated before, the chief points of agreement between the two being: (1) the general form and colours of the body, (2) the almost complete fusion of the infra-intestinal ganglion with the visceral one, (3) the notched cusp of the radular teeth, (4) the elongated tubular crop, and (5) the folliculated oesophageal diverticulum. In *L. serradifalci,* however, there has yet been no mention by any author of the black streaks which are usually found on the mantle in the recorded specimens of *L. souverbii.* When the two are regarded in the future as conspecific, the former has priority over the latter.

ACKNOWLEDGMENTS

The main material for this study was presented by Dr. Terufumi Yamasu of the Tamano Marine Laboratory, Okayama University, to whom I am particularly indebted.

I wish to extend my thanks to the Chief of the Biological Laboratory, Imperial Household, and to Mr. Iwao Hamatani of the Osaka Kyoiku University for offering me additional data for a comparative study; and to Mr. Gale G. Sphon of the Los Angeles County Museum of Natural History for his personal communication concerning a new idea of identification of the world species of *Lobiger.*

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On the Identity of *Murex triqueter* Born

(Gastropoda : Muricidae)

BY

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(1 Plate; 2 Text figures)

IT WAS FIRST CALLED to my attention by Anthony D'Attilio of the San Diego Natural History Museum that there were 2 Indo-Pacific species being identified as *Murex triqueter* Born, 1778. Mr. D'Attilio sent me the radula drawing reproduced here (Figure 4) and noted (*in litt.*) "This radula doesn't look quite like the one figured by Cernohorsky [reproduced here, Figure 5], Veliger, v. 10, no. 2, p. 125, fig. 6, shell on plt. 15, fig. 15. It is my idea from having studied *triqueter* that there is another very similar though distinct species. The two sometimes occupy the same geographic range but at times do not, or if they do the one species is more common. In the Indian Ocean and East Africa the true *triqueter* is very common, though the other species turns up rarely. In the South Pacific, *i. e.*, Queensland, Fijis, Solomons, the other is the commonly occurring species. In the Philippines both forms occur also, although I have the impression that *triqueter* is less common. Both also occur in Okinawa. Do you know of a name for the other species?"

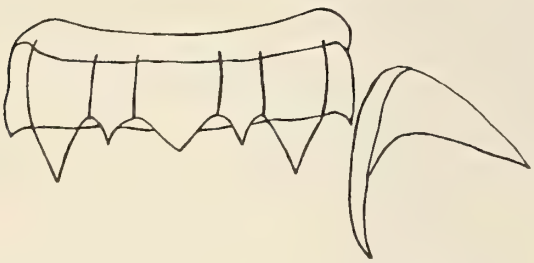

Figure 4

Chicoreus (Naquetia) triqueter (Born, 1778)
Drawing of radula by Anthony D'Attilio

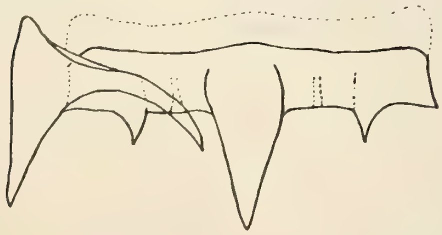

Figure 5

Chicoreus (Naquetia) trigonulus (Lamarck, 1816)
Drawing of radula after CERNOHORSKY, 1967, text figure 6

Subsequent investigation indicated that his assessment was correct and also revealed an undue amount of confusion between the 2 forms. My questioning (VOKES, 1970: 184) of CERNOHORSKY's (1967: 124) identification of a Fijian shell as *Murex triqueter* led to his (CERNOHORSKY, 1971) figuring the type of certain other species involved, and greatly facilitated the ultimate resolution of the problem.

The morphological differences between the 2 species seem to be constant, although there is some intergrading. But, in general, it may be said that one of these species, which will be referred to as the "Indian Ocean form," is characterized by a marked roughness of shell texture with the varical flange noticeably squamose, this latter being the most easily observed difference in the 2 species. The color tends to be darker, with often an overall brown color rather than the maculated appearance of the other species. The second, which will be called the "Pacific form," has a smoother shell, marked by a cancellate sculpture composed of distinct spiral cords, crossed by narrow axial ridges. Where the axial ridges meet the sutures there are peculiar buttress-like structures similar to those usually associated with the members of the genus *Aspella*. The varical flange is composed of a single lamina and is not squamose. The length of the body whorl in proportion to the height of the spire is much greater in the Pacific form,

being on the order of 2:1, while the Indian Ocean form is approximately 1.5:1. As a result of this factor the aperture of the Pacific species is more oval than is that of the Indian Ocean form. The operculum of the latter is a darker brown color. The most convincing difference, however, as noted by Mr. D'Attilio, is the different radulae possessed by the 2 species (compare Figures 4 and 5).

Both forms have been referred to *Murex triqueter* by various authors. Obviously one of them is *M. triqueter* and the other is not. There are several possible names, but first we must ascertain which is, in fact, the true *M. triqueter* and which is "the other."

The root of the problem lies in the original description of *Murex triqueter* by Born. Born published two works, the first in 1778, entitled *Index rerum naturalium Musei Caesarei Vindobonensis.* In this work he listed a number of species, some of which were Linnaean and others which were new. The new species are not illustrated but, as was the custom of the times, bear references to previous illustrations in various iconographies. For his new species *Murex triqueter* there is a reference to Martini's *Conchylien-Cabinet,* v. 3, fig. 1038, a shell there denominated as "Purpura subalata, triquetra, variegata" and stated to be from the East Indies and Tranquebar. The shell, illustrated, unfortunately, only from the dorsal side, is the Indian Ocean species.

In 1780 Born published a second work entitled *Testacea Musei Caesarei Vindobonensis* and in this new edition he provided illustrations of his species based upon actual specimens in the Museum of the Kings of Vienna, now the Naturhistorisches Museum of Vienna. The specimens are still in the Museum and through the kindness of Dr. Oliver E. Paget I obtained a photograph of the specimen illustrated by Born. It is the Pacific species (see Figure *1*). Subsequent writers can scarcely be blamed if the 2 forms have been confounded. Most writers have resolved the dilemma by placing the 2 forms in synonymy, which does make everything much simpler. However, inasmuch as both Mr. D'Attilio and I, at least, are convinced that there are two distinct species involved, the question then becomes which of the two is *Murex triqueter* Born?

The question of whether a reference to a published figure is to take precedence over a "type specimen" is one that has bothered taxonomists for many years. The species of Linnaeus are particularly complicated in this fashion. Entire books have been written attempting to identify the Linnean species (*e. g.,* Hanley, 1855; Dodge, 1952 to 1959) but other early workers were little better. It was frequent to cite a previously published figure rather than to provide a new one because of the added expense of the engravings, if nothing else. In the case of Linnaeus often there are 3 or 4 references to as many species (sometimes genera) and establishing exactly which of these is to bear the name is difficult. When there is a single reference the problem is less complicated. But, nevertheless, specimens often have appeared later that are considered as part of the original type lot of the writer in question and frequently these do not agree with the figure that was the original reference for the species. In such a case what are we to do?

I once raised just this question before the International Commission on Zoological Nomenclature in connection with another species, and was told by Margaret Spillane (*in litt.*): "The type series includes previously published figures (Art. 73c(i)) and the specimens represented by such figures may be designated as lectotypes (Art. 74b). Does this not answer your query?" Article 73c(i) of the Code cited by Miss Spillane reads: "Syntypes may include ... specimens not seen by the author but which were the bases of previously published descriptions upon which he founded his taxon in whole or in part." Article 74b adds that "Designation of a figure as a lectotype is to be treated as designation of the specimen represented by the figure; if that specimen is one of the syntypes, the designation as lectotype is valid from the nomenclatural standpoint." Therefore it is completely valid and legal to designate the specimen represented by the figure in Martini, v. 3, fig. 1038, a specimen stated to have been in the collection of Martini at the time, although I do not know where it presently resides, as the lectotype of *Murex triqueter.* The presence of a specimen in the Vienna Museum that is of a different species in no way countermands this selection for both the figure and the specimen are syntypes and, as such, both were equally available to be selected as lectotype. Had the Museum specimen been figured at the same time as the reference to the Martini figure, I would have suggested selecting the specimen, but in view of the 2 year's difference in the 2 publications it would seem that the figure has "priority." It is most probable that Born, as have many others later, considered the 2 forms as the same species, and hence it becomes a matter of restricting the name *M. triqueter* to one form or the other. I here select the first, with the type locality Tranquebar, as stated by Martini.

If there were any solid agreement among subsequent authors as to which form were to bear the name *triqueter,* I would have also been influenced by this factor. But certainly this is not the case. Röding (1798), interestingly, seems to have realized very early that there were 2 species involved. These he named *"Purpura" variegata* and *"Purpura" cancellata.* There is no doubt that he was attempting to distinguish between the 2 forms under discussion, as he cites *P. variegata* (in German) as the "checkered purple-snail," and *cancellata* as the "cancellate purple-snail."

Unfortunately he had only the single Martini figure for reference and so he employed it for both species, not anticipating the restrictions of latter-day nomenclators, and thus both of his names are objective synonyms of *Murex triqueter.*

Perry (1811), who recognized the previous species of no authors (although many of his species carry Linnaeus and Gmelin names), gave the Indian Ocean form a new name, *Triplex flexuosa,* with the locality as "New Zealand," a slightly erroneous assignment. Were the type of *Murex triqueter* picked to be the thin-flanged Pacific form, this name would be the first available for the Indian Ocean species.

In 1816 Lamarck published the illustrations of the *Encyclopédie Méthodique* (as *Tableau Encyclopédique et Méthodique*), although the text was not to appear for many years. However, there was a list of names accompanying the plates and the species figured therein date from "La Liste," as it is known. In this work we find a new species, *Murex trigonulus* Lamarck, that enters into our discussion. The ramifications of the identity of this species have been discussed in a previous work (Vokes, 1968a) but it will be necessary to repeat some of the data to make the entire history of *M. triqueter* intelligible.

Briefly, in 1816 Lamarck figured 2 species, one of which (plt. 417, fig. 1), cited as "*Murex triqueter* Born," is actually a specimen of the Caribbean *Chicoreus (Siratus) consuela* (Verrill, 1950), better known by the preoccupied name *Murex pulcher* Adams. The second species (plt. 417, fig. 4) Lamarck named *Murex trigonulus.* In 1822, Lamarck decided he was in error and placed the 1816 figure of his *M. trigonulus* in synonymy with *M. triqueter,* changing the other species (*i. e.,* the one that he had originally called *triqueter*) to a "variety b" of *M. triqueter.*

For some unknown reason Kiener, in 1842, chose to return to the 1816 designations rather than to employ the 1822 corrections and thus we find "*M. triqueter*" (plt. 40, fig. 3) is a fine example of *Chicoreus consuela,* and "*M. trigonulus*" (plt. 25, fig. 2) is the Indian Ocean species under discussion. In view of the fact that Cernohorsky (1971, fig. 3) has recently figured one of the syntypes of Lamarck's *M. trigonulus* [1] we now know what species originally was considered as *M. trigonulus* by Lamarck, although not by Kiener. The 1816 Lamarck illustration is somewhat ambiguous but it does emphasize the spiral cords that are characteristic of the Pacific species, whereas it is the axial ridges that are more pronounced in the Indian Ocean form. Deshayes (1832: 901), who finally published the text of the *Encyclopédie,* notes that Lamarck's plate 417, figure 4, "*Murex trigonatus*" (just to add further to the confusion) is a synonym of *M. triqueter.* From his description there is no doubt that Deshayes is describing the Indian Ocean shell, as he states that the last varix "est dilatée en aile assez mince et profondément plissée. Les plis sont écailleux en dessous." As in the case of Born, Lamarck probably had specimens of both species, and undoubtedly in the collections of the Paris Museum, studied by Kiener, there were both forms. Clearly Lamarck thought both were the same when he placed his *trigonulus* into synonymy with *triqueter.*

In 1822, Lamarck considering that the name *Murex trigonulus* was no longer being used, and was therefore free, reemployed it for another species, and it is this one that is frequently cited by authors as "*Murex trigonulus* Lamarck." I have discussed the identity of this species (Vokes, 1968a) and concluded that the species in question is that one later named *Pterynotus annandalei* Preston, 1910.

Cernohorsky's figuring of the specimen in the Muséum d'Histoire Naturelle, Geneva, no. 1099/35, as the only extant syntype and presumably, therefore, lectotype of the species has the effect of restricting the name *Murex trigonulus* Lamarck to the Pacific species. It was this selection in a large measure that influenced my subsequent

[1] During the process of attempting to resolve the problem of identities the following information was sent from Dr. E. Binder, of the Muséum d'Histoire Naturelle, Geneva, to Dr. William K. Emerson, American Museum of Natural History, New York (1962, *in litt.*):

> "I send you two photographs of the possible type of Lamarck's *Murex trigonulus.* It was in Lamarck's collection, labeled '*M. triqueter* Born var.', but this may be a 'rectification' by a subsequent curator. I think it is the specimen figured in the Encyclopédie Méthodique Pl. 417, fig. 4 a&b. Its length is 38 mm; Lamarck indicates 18 lignes = $40\frac{1}{2}$ mm.
>
> "If there had been any specimens in Lamarck's collection clearly labeled '*Murex trigonulus*', I would have had no trouble in finding out which was the Type. But there are no specimens so labeled.
>
> "Since Lamarck considered all his specimens figured in Encyclopédie Pl. 417 fig. 1 a&b and fig. 4 a&b as one and the same species, and they are certainly not *M. triqueter* Born, he must have made an error somewhere. It seems logical to think that these specimens might possibly be what Lamarck had first called *M. trigonulus,* and that by a later mistake he has attributed them to *M. triqueter.* This suspicion is reinforced by the fact that Kiener, who worked on Lamarck's collection, inverted both species.
>
> "I think this is the most likely definition one can give of *M. trigonulus,* but of course you do not have to adopt it."

This would seem to confirm the writer's opinion that Lamarck somehow changed his mind over the identity of his *Murex trigonulus* between 1816 and 1822. However, this would not affect the identity of the species originally given the name, once figured the species so named was committed to posterity for better or for worse.

selection of the Indian Ocean form to bear the name *Murex triqueter.* Thus both forms are well-established and the only remaining problem is to sort out the subsequent synonymy of the 2 species involved.

At the end of this paper I have a synonymic list for each of the 2 species; however, it should be noted that the references included are only those that have figures, or are otherwise clearly one form or the other. Simple citations of *"M. triqueter"* or *"M. trigonulus,"* without means of determining definitely which form is under consideration, are omitted.

As noted above, many writers, both early and late, have considered the 2 forms to be one species. Reeve, in the *Conchologica Iconica* (1845) was the first author to give a good figure of *Murex triqueter* under that name (plt. 1, fig. 4), noting "The *Murices triqueter* and *trigonulus* are figured in the 'Encyclopédie Méthodique' and in Kiener's 'Icon. Coq. Viv.' one for the other, and *vice versa.*" Accordingly, he figured as *"M. trigonulus"* a magnificent specimen of *Chicoreus consuela* (plt. 22, fig. 17).

A. Adams may have been the first to realize that there were 2 species involved for he named *Murex cumingii,* which he stated was "somewhat closely allied with the *M. triquetra* of Born" (1853: 270), and in his description he emphasizes "labro ... fimbriato, fimbriis non squamulosis." In 1879, Sowerby, in the *Thesaurus Conchyliorum,* gave a good illustration of the Indian Ocean *M. triqueter* (fig. 114) and also a "variety *cumingii*" (fig. 115), indicating that he recognized a difference. CERNOHORSKY (1971, fig. 4) has also figured the lectotype of *M. cumingii* and it is obviously the same as *M. trigonulus,* named as new by Adams no doubt because of the confusion of true *M. trigonulus* with *M. triqueter.*

Tapparone-Canefri in his study of the mollusks of Mauritius (1881) compared *Murex cumingii* with *M. triqueter* and concluded that the 2 could be separated: "1° par sa forme générale ... la spire [of *M. cumingii*] est plus courte relativement au dernier tour, l'ouverture est également plus grande et de forme ovale-allongée et non arrondie; 2° par la forme et la texture des varices, qui ne sont point saillantes et pas du tout épineuses; 3° par la coloration, qui est assez différente."

Among modern workers Habe seems to be the only one who has correctly identified these 2 species. Initially, in the Japanese edition of *Coloured Illustrations of the Shells of Japan* (II) HABE (1961) figured the Pacific species under the name *Naquetia triqueter* (plt. 25, fig. 13) but in the later English edition (HABE, 1964) of the work, entitled *Shells of the Western Pacific in Colour,* v. 2, he changed the identification to *Naquetia trigonalis* (Lamarck) [sic], and in 1966 HABE & KOSUGE, in *Shells of the World in Colour,* v. 2, *The Tropical Pacific,* figured an example of the Indian Ocean shell, as *Naquetia triqueter* (p. 56; plt. 20, fig. 15), noting that the species is widely distributed south of the Philippines and in the Indian Ocean. They add that, although it resembles *N. trigonulus,* it may be clearly distinguished by the brown axial ridges.

There is another species, described from the Philippines by Sowerby, that may be a synonym of *Murex trigonulus.* This is *M. roseotinctus,* which SOWERBY (1860: 429) described as "resembling *M. trigonulus* but wanting the expanded fringe at the lower part of the fronds of that species." The color is a beautiful pink, and in general shape the shell seems closer to the *Pterynotus annandalei* mentioned above, which to Sowerby was *"M. trigonulus,"* than to the true *M. trigonulus.* The species, which has not been recognized since its description, most nearly resembles the Caribbean *Chicoreus (Siratus) consuela,* suggesting possible mistaken locality data.

I would like to state that I too have been as confused as any by these 2 forms and in 1968 I figured a specimen of *Murex trigonulus* as *M. triqueter* (VOKES, 1968a: plt. 13, figs. 3, 4), because I did not realize that there were 2 species involved. When Mr. D'Attilio first raised the question of "What is the name for the other?" I began to investigate, and, from the distribution data, plus the fact that CERNOHORSKY (1967: p. 124) had placed *M. triqueter* var. *amanuensis* Couturier, 1907, in synonymy with the species he figured as *"M. triqueter"* (*ibid.,* plt. 15, fig. 15), which was the Pacific form, and from Couturier's statement that his Tahitian shell differed from the type by the more slender and elongated anterior canal, I came to the conclusion that *amanuensis* was the first available name for the Pacific form, believing erroneously that *M. trigonulus* was the same form as *M. triqueter* (having been led astray by Kiener and Deshayes, as well as Lamarck).

Murex triqueter Born was named as the type of the genus *Naquetia* Jousseaume, 1880. Regardless of which form is taken to be the true *N. triqueter,* the generic concept is not changed. I have previously considered *Naquetia* to be a subgenus of *Pterynotus,* but in the course of preparing the present paper, I have come to realize that *Naquetia* is more closely allied with *Chicoreus.* My reason for this change of opinion is that I had the opportunity to see a juvenile specimen of *N. triqueter* and from the nature of the early development it is obviously of the *Chicoreus* group rather than the *Pterynotus* group. I have discussed these 2 basic lineages of Muricidae in other papers (*e. g.,* VOKES, 1968b: 86) and it can be seen that there are two very fundamental types of early development observed in the Muricinae. One of these is the type found in the *Pterynotus-Poirieria* line where, on the first post-nuclear whorl, there are 6 small fin-like

varices. In *Pterynotus* every other one of these disappears on the second or third teleoconch whorl, leaving 3 varices and 3 intervarical nodes per whorl. In *Poirieria, Paziella,* etc., these 6 varices simply persist to the adult stage. But in the *Hexaplex-Chicoreus-Murex s. s.* lineage the early development is totally different. On the first post-nuclear whorl there are 12 small axial ribs, and on succeeding whorls certain of these change into small spinose or foliaceous varices, 3, 4, 6, or more to a whorl, with the others remaining as intervarical nodes. The juvenile *N. triqueter* has this latter type of development with, on the second teleoconch whorl, every 4th rib becoming a varix and the intervening 3 becoming intervarical nodes. This pattern persists up to the adult stage. Furthermore, the young *N. triqueter* has spines on the shoulder and on the siphonal canal, as seen in *Chicoreus.*

The second factor that influenced my change of generic assignment is the nature of several allied species, in particular, *"Murex" laciniatus* Sowerby, which usually appears to be a *Chicoreus* but in extreme individuals may develop an expanded wing-like flange on the anterior canal that looks exactly like *Naquetia.* Certain other members of *Naquetia,* especially *"Pterynotus" annandalei,* tend to merge with the members of the subgenus *Chicoreus (Siratus),* but in the latter group there is no varical flange along the anterior canal, which is usually greatly extended. Thus the species *"Murex" superbus* Sowerby, 1889, and *"Murex" consuela* Verrill are assigned to *Siratus,* in spite of a marked affinity to *"M." trigonulus* and *"P." annandalei,* because they have spines on the siphonal canal rather than a flange.

I am of the opinion that the different lineages of *Chicoreus, i. e., Phyllonotus,* and *Siratus,* and now *Naquetia,* are all probably more closely related to each other than they are to *Chicoreus.* Again we are confronted with the familiar problem of the oldest generic name not necessarily being the oldest morphotype. In the early stages of evolution *Phyllonotus* and *Chicoreus* are much more closely akin than are the modern forms. The morphotype that has been given the name *Torvamurex* (type: *Triplex denudatus* Perry) is the more normal "ancestral" *Chicoreus,* and its relationship to the other subgenera is more obvious than the *Chicoreus* typefied by *C. ramosus* with its elaborate frondose varices.

The geologic history of these various lines is not completely known but all indications at present are that in the New World *Phyllonotus* was derived from a *Hexaplex* ancestor during the Oligocene, and *Siratus,* in turn, developed from a *Phyllonotus* ancestor. At the same time *Chicoreus s. s.* was also being derived, and as there are no members of *Phyllonotus* known from the central European area where the oldest *Chicoreus* appears, in all probability *Chicoreus* and *Phyllonotus* represent parallel but separate diversions. The oldest known *Chicoreus s. s.* (*Murex nudus* Noszky) is from the Oligocene of Hungary and looks very little different from the earliest *Phyllonotus.* However, in the Miocene of the European region the line develops into true *Chicoreus* and in the New World it develops into *Phyllonotus.* If the modern species of *Phyllonotus* were not so distinctive, the early members would be just as easily placed in *Chicoreus s. s.*

The species I have considered to be the ancestral *Naquetia, "Murex" williamsi* Sokolov, is totally different from this *Phyllonotus*-like form and evidently represents a distinct line of evolution. (It is entirely possible that the resemblance between *"Murex" williamsi* and *"Murex" trigonulus* is coincidental and this species from the Upper Eocene of Ukrainia is not actually related to the *Naquetia* line.) Unfortunately nothing is known of the nature of the early whorls of this fossil species, but the cancellate ornamentation suggests that the early whorls are like those of the other *Naquetia* species. If this species is, in fact, the progenitor of the *Naquetia* line, in all probability the species of *Chicoreus (Siratus)* seen in the Pacific region are separately derived from this line and are not closely related to the western Atlantic species of *Siratus.* The phylogenetic development of these groups would seem to give credence to the statement often made that there is no such thing as a "phylogenetic tree" but rather we have phylogenetic "reticula" or nets. It would appear that *Na-*

Explanation of Figures *1* to *3*

Figure *1*: *Murex triqueter* Born, 1778. Syntype, Naturhistorisches Museum, Vienna, no. NHMW 76.566. Height 53.1 mm, diameter 22.0 mm (× 1½, approximately). Photograph courtesy Dr. Oliver E. Paget, Naturhistorisches Museum, Wien.
Figure *2*: *Chicoreus (Naquetia) triqueter* (Born, 1778). Hypotype. Height 70.0 mm, diameter 29.0 mm (× 1½). Rabaul, New Britain.
Figure *3*: *Chicoreus (Naquetia) trigonulus* (Lamarck, 1816). Hypotype. Height 60.0 mm, diameter 27.3 mm (× 1½). Guam, Mariana Islands.

Figure 1a

Figure 1b

Figure 2

Figure 3

quetia is the Indo-Pacific equivalent of the western Atlantic *Phyllonotus-Siratus* group and within both lines a *Siratus*-like form has appeared, which today we cannot separate on purely morphologic grounds.

The Pacific *Siratus*-like form has been given another generic name, *Chicomurex* Arakawa, 1964 (type species: *Murex superbus* Sowerby), originally separated from *Chicoreus s.s.* on the basis of the different radula. However, the radula of *"Chicomurex" superbus*, as figured by Arakawa (1964: plt. 21, figs. 5, 6) is very close to the radula seen in species of *Phyllonotus* and *Siratus* (Radwin and D'Attilio, *in litt.*) and as there is no other basis for separation, except perhaps the paleontologic record, I consider *Chicomurex* a synonym of *Siratus*. There are several undescribed species in the Indo-Pacific region that approach the morphology of *Phyllonotus* and these also, I assume, represent parallel evolution.

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Chicoreus (Naquetia) triqueter (Born, 1778)

(Figures *2* and 4)

1777. *Purpura subalata, triquetra, variegata* Martini, Neues Syst. Conchylien-Cab. 3: 350; plt. 111, fig. 1038
1778. *Murex triqueter* Born, Index. Mus. Caes. Vindob.: 288
1811. *Triplex flexuosa* Perry, Conchology, plt. 7, fig. 1
1839 - 1868. *Murex triqueter* Born, Küster, Syst. Conchylien-Cab. Martini and Chemnitz, 3 (2): 29 [1856], plt. 12, fig. 7 (copy of Martini, plt. 111) [1839]; plt. 20, fig. 4 [1868]
1842. *Murex trigonulus* Lamarck, Kiener, Icon. Coq. Viv. 7: 119; plt. 25, fig. 2 (not of Lamarck, 1816)
1845. *Murex triqueter* Born, Reeve, Conch. Icon., 3: plt. 1, fig. 4
1879. *Murex triqueter* Born, G. B. Sowerby 2nd, Thes. Conch. 4: 9; fig. 114
1880. *Murex triqueter* Born, Tryon, Man. Conch. 2: 85; plt. 40, fig. 506 (after Reeve)
1966. *Naquetia triqueter* (Born), Habe & Kosuge, Shells of the World in Colour 2: Tropical Pacific: 56; plt. 20, fig. 15

Chicoreus (Naquetia) trigonulus (Lamarck, 1816)

(Figures *1, 3,* and 5)

1780. *Murex triqueter* Born, Test. Mus. Caes. Vindob.: 291; plt. 11, figs. 1, 2
1816. *Murex trigonulus* Lamarck, Tabl. Encycl. Méth. (Vers), plt. 417, figs. 4a, 4b; Liste, p. 5
1853. *Murex cumingii* A. Adams, Proc. Zool. Soc. London, pt. 19: 270
1879. *Murex triqueter* var. *cumingii* Adams, G. B. Sowerby 2nd, Thes Conch. 4: 10; fig. 115
1907. *Murex triqueter* var. *amanuensis* Couturier, Journ. de Conchyl. 55: 142
1953. *Murex (Pteronotus) triqueter* Born, M. Smith, Illust. Cat. Rock Shells: 4; plt. 4, fig. 4
1957. *Pyerynotus triquetor* [sic] (Born), Kaicher, Indo-Pacific Sea Shells, Muricacea, Buccinacea: plt. 2, fig. 7
1961. *Naquetia triqueter* (Born), Habe, Coloured Illust. Shells of Japan (II): 50; plt. 25, fig. 13
1964. *Naquetia trigonalis* [sic] (Lamarck), Habe, Shells Western Pacific in Colour 2: 80; plt. 25, fig. 13 (same figure as Habe, 1961)
1967. *Pterynotus (Naquetia) triqueter* (Born), Cernohorsky, Veliger 10: 124; plt. 15, fig. 15; text fig. 6
1967. *Pterynotus triqueter* (Born), Cernohorsky, Marine Shells of the Pacific: 126; plt. 26, fig. 160; text fig. 13
1968. *Pterynotus (Naquetia) triqueter* (Born), Vokes, Journ. of Conch., 26: 302; plt. 13, figs. 3, 4
1970. *Pterynotus (Naquetia) amanuensis* (Couturier), Vokes, Veliger 13: 184
1971. *Murex trigonulus* Lamarck, Cernohorsky, Veliger 14: 189; fig. 3 [Syntype]
1971. *Murex cumingii* A. Adams, Cernohorsky, Veliger 14: 189; fig. 4 [Lectotype]

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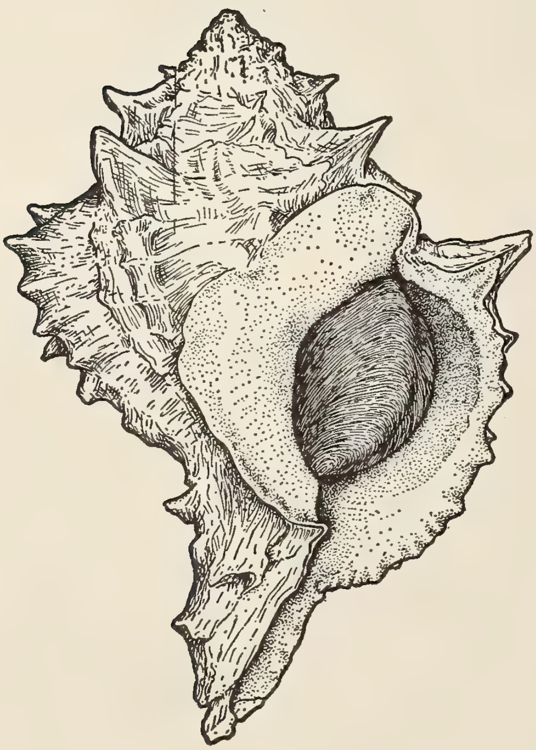

Self-Fertilization in the Terrestrial Snail *Rumina decollata*

BY

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(1 Text figure)

INTRODUCTION

STUDIES OF ALLOZYMIC VARIATION in *Cepaea* (MANWELL & BAKER, 1968; LEVAN & FREDGA, 1972), *Helix* (SELANDER & KAUFMAN, 1973b), *Partula* (SCHWABL & MURRAY, 1970) and other genera (KAUFMAN & SELANDER, 1973) have demonstrated that many terrestrial pulmonate snails are highly polymorphic at structural gene loci encoding enzymes. However, populations of the achatinid species *Rumina decollata* (Linnaeus, 1758) are largely or entirely monomorphic. In its native Mediterranean range, *Rumina* exists as a large series of distinctive strains, but North American populations, which were derived from an introduction prior to 1822, apparently represent a single monogenic strain, for no genic variation was detected in an assay of 25 enzymes in 754 individuals from 23 localities (SELANDER & KAUFMAN, 1973a).

The surprising results of our allozymic analysis of *Rumina* suggested that self-fertilization is a major mode of reproduction, since very close inbreeding is the most likely cause of severely reduced heterozygosity in large, continental populations. As a test of this hypothesis, we reared individuals in isolation to determine whether cross-fertilization is necessary for reproduction. Our results, herein reported, indicate that the unusual monogenic structure of *Rumina* populations is, in all probability, generated by a breeding system of facultative self-fertilization.

MATERIALS AND METHODS

Eggs were obtained from a group of 150 adult *Rumina* collected at 5 localities in and around Austin, Texas, and maintained in large plastic cages. On May 30, 1972, several hundred eggs laid on May 29 were collected and incubated at room temperature in lots of 25 between sheets of paper towel moistened with de-ionized water in 50×10 mm Petri dishes. The incubation period under laboratory conditions is about 30 days. On June 28 and 29, 105 eggs that obviously were ready to hatch (as evidenced by their distinctive color and the thinness of their shells) were isolated singly in 50×10 mm Petri dishes containing moist filter papers; and 68 pairs of eggs were similarly isolated. When the eggs hatched one or two days later, the snails were supplied with lettuce, carrot, rolled oats, and calcium carbonate. There was no mortality in the juvenile stage. After the juveniles were ½ inch (12 mm) long, they were maintained in 100×20 mm Petri dishes. Throughout the period of the experiment, the singles and pairs were transferred to clean dishes and given fresh food every 3 days.

Pair-members and singles began laying eggs on September 9 and 13, respectively. All eggs were counted and most "clutches" were incubated at room temperature between moist paper towel in individual Petri dishes. After 30 days of incubation, the number of eggs hatched in each clutch was counted and all unhatched eggs were broken and scored as (1) ready to hatch (containing a living snail similar in size to those already hatched), (2) containing small or medium-sized embryos (dead or abnormally slow in development), or (3) infertile (no conspicuous evidence of embryonic development).

The experiment was terminated on November 9, but several dozen eggs laid by singles were hatched in isolation to continue the selfing line into the second generation.

RESULTS

Body Weight

Growth was rapid but highly variable in rate in both singles and pair-members until the time of laying. In 64 singles weighed on October 9 and again on November 9, there was a 9% **decrease** in mean weight, perhaps owing

to decollation (shedding of terminal whorls). Mean weights were 1.496g and 1.356g, respectively ($t_{(63)} = -7.70$, $P < 0.001$). Similarly in the same period, 42 pair-members showed a 3% decrease in mean weight, from 1.049g to 1.019g ($t_{(41)} = -3.08$, $P < 0.01$). Three very small pair-members (P55a, P59a, and P63a) died late in the experiment, never having reached a weight greater than 0.30g. In the 133 pair-members surviving to the end of the experiment, mean body weight was 1.155g. And mean body weight of the 105 individuals reared singly was 1.322, or 11% greater ($t_{(236)} = 3.15$, $P < 0.01$). Coefficients of variability were similar in singles (28.0%) and pair-members (27.3%).

The smaller average body size (as reflected by weight) of pair-members may be attributed to a combination of factors. Food (including calcium carbonate) may periodically have been in shorter supply for pairs, even though we attempted to maintain it in excess at all times. The greater accumulation of wastes in Petri dishes containing pairs may also have retarded growth either directly or by inhibiting feeding, for we have noted that *Rumina* tends to become inactive as the food becomes stale and wastes accumulate. Finally, the earlier onset of full production of eggs in pair-members (see beyond) may have caused an earlier termination of the rapid growth phase. Unfortunately, however, we cannot assess such a relationship among the pairs, since we do not have dates of first laying for **individual** pair-members, only for the pairs as such. Among the singles, there may be a weak **negative** regression of body weight on date of first laying ($F_{(1,104)} = 3.64$, $0.05 < P < 0.10$).

Because the *Rumina* populations from which our experimental individuals were derived are demonstrably monomorphic at a randomly selected sample of 25 structural gene loci (SELANDER & KAUFMAN, 1973a), it is probable that the great majority of, if not all, loci are similarly monomorphic. If so, most or all phenotypic variance must be environmentally induced, and we would expect adult body size of pair-members raised together to be correlated, inasmuch as the environment is similar for both individuals. And in fact body weights of pair-members were strongly correlated, with $r_{(63)} = 0.746$ ($P \ll 0.001$). This degree of relationship is all the more remarkable considering the rather sizable contributions to variance in body weight made by decollation and by the variable number of eggs in the uterus at the time of weighing.

Egg Production

In the following account, egg production is expressed in terms of eggs laid per day. Egg production was recorded for approximately 2 months after the first member of each experimental group laid, that is from September 9 to November 6 for pairs, and from September 13 to November 13 for singles. Except for singles or pairs laying late in these periods, we have data on egg production for approximately 2 months. Because eggs were not gathered and counted daily, the actual length of a "month" varies among individuals and pairs.

Pairs. Most pairs (one or both individuals) began laying in a two-week period beginning on September 9, and the mean date for all pairs was September 19. As shown in Figure 1, there is no relationship between date of first laying and rate of egg production in the first month. On the average, individual pair-members laid 1.432 eggs per day in the first month and 1.811 eggs per day in the second month (Table 1).

Table 1

Pairs: Mean egg production and hatching success

Period of first laying	Number of pairs	Production: eggs/day First month	Production: eggs/day Second month	Hatching success in first month Total	Hatching success in first month Last $\frac{2}{3}$ of eggs laid
September 9 - 14	20	3.30	3.58	0.734	0.821
September 15 - 21	25	2.58	3.62	0.602	0.700
September 23 - October 20	20	2.16	3.70 (11)	0.667	0.720 (16)
Pooled					
per pair	65	2.864	3.621 (56)	0.6593	0.7451 (61)
per individual	130	1.432	1.811 (112)		

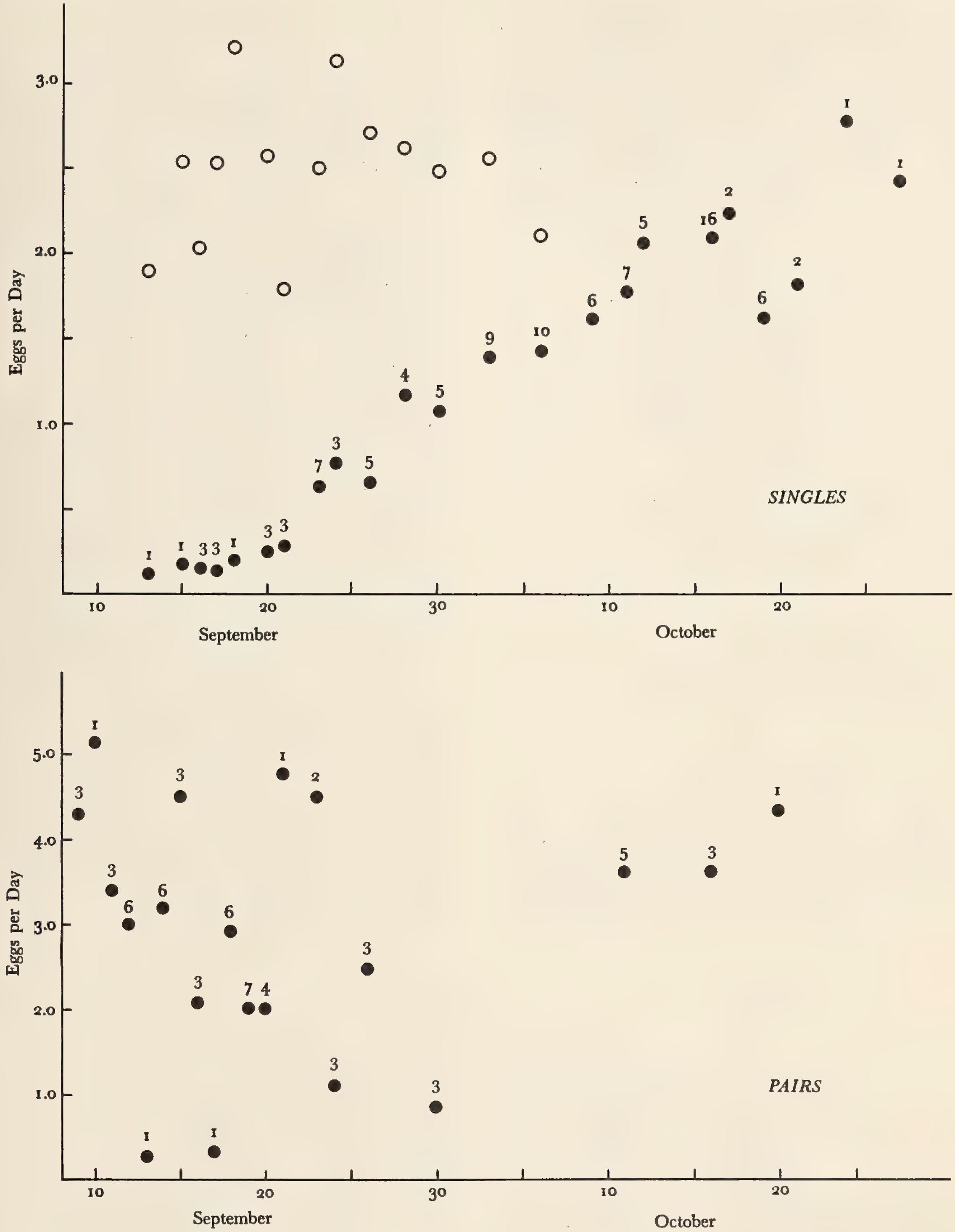

Figure 1

Rate of egg production (eggs/day) as a function of date of first laying by singles (top) and pairs of *Rumina decollata*. For singles, dots indicate rate of production in first month and circles indicate rate in second month. For pairs, dots indicate rate in first month. Plotted points are mean rates for indicated numbers of singles or pairs.

Singles. Date of first laying by singles ranged from September 13 to November 6, a span of 7 weeks. Unlike the situation in the pairs, the rate of egg production in the first month was related to initial laying date (Figure 1). The first 7 singles to lay produced less than 0.3 eggs per day in the first month, but with successively later initial dates production in the first month gradually increased. The last individuals to begin laying late in October immediately produced at high rates not achieved by the earlier-laying singles until their second month. Although the mean date of first laying for all singles was October 5 (and for the first 63 singles laying, September 25), none of the singles achieved full production until mid-October. Individuals laid an average of 1.316 eggs per day in the first month but increased production to 2.446 eggs per day in the second month. The rates of egg production of singles in the first and second months were not correlated.

Clutch sizes in the singles increased gradually for several weeks (early layers) or days (late layers) to stable levels; thereafter there was remarkably little interclutch variation. The distribution of these stabilized clutch sizes for 103 singles was as follows:

Clutch size:	5	8	9	10	11	12	13	14	15	16
Number of singles:	1	3	4	5	20	20	27	19	3	1

Median clutch size falls between 12 and 13; the mean is 12.2; and for 84% of individuals clutch sizes fall in the range 11 to 14.

Hatching Success

Pairs. The 65 pairs surviving to the end of the experiment produced a total of 5099 eggs in their first month of laying. Of these, 3448 were incubated. Hatching success for the total month and for the last $\frac{2}{3}$ of the eggs laid by each pair in the month is shown in Table 2. (Because eggs laid in the second month were not incubated, we do not have estimates of hatching success beyond the first month.) Characteristically, hatching success of the first 2 or 3 clutches from each pair was poor, with the result that mean hatching success of the last $\frac{2}{3}$ of eggs laid is significantly higher than that of all eggs laid in the month.

All but one of the 65 pairs laid eggs that hatched. The exceptional pair (P51, first laying on September 26) produced a total of 87 eggs, 52 of which were incubated. All failed to hatch, but 11 contained small embryos. Hence all 65 pairs produced fertilized eggs.

Hatching success for all eggs laid by the 65 pairs taken as a single group was 0.667, a value close to the mean for pairs shown in Table 1.

Singles. The 105 singles laid a total of 6822 eggs, of which 4313 were incubated. Only 3 singles failed to lay eggs that hatched: S97 laid 37 eggs, beginning on October 19; 21 were incubated, of which only 2 contained embryos. S98 laid 8 eggs, beginning on October 19; all were abnormally small and infertile. S105 laid last, one infertile egg on November 6. Thus all singles but 2 laid fertile eggs. In calculating hatching success, data for S105 were omitted.

Early-laying individuals had poor hatching success (0.531) in the first month, but there was a marked improvement in the second month (Table 2). Mean hatching success for all singles increased from 0.671 in the first month to 0.778 in the second month.

Hatching success for all eggs laid taken as a single group (0.7422) was similar to the mean for individuals shown in Table 2.

Of the eggs that failed to hatch, 69% were infertile, 23% had small embryos, and 8% had medium-sized embryos. There was no significant difference in these proportions between singles and pairs.

Table 2

Singles: Mean egg production and hatching success

Period of first laying	Number of singles	Production: eggs/day First month	Production: eggs/day Second month	Hatching success First month	Hatching success Second month
September 13 - 26	30	0.43	2.49	0.531	0.737
September 28 - October 6	28	1.31	2.39	0.753	0.826 (26)
October 9 - November 6	47	1.88	—	0.709 (46)	—
Pooled	105	1.316	2.446	0.6713 (104)	0.7784 (56)

DISCUSSION

The results of our experiment demonstrate that cross-fertilization is not required for reproduction in *Rumina decollata,* and that the capacity to produce fertile eggs without cross-fertilization is shared by all or nearly all individuals. Because genetic markers were not available when our experiment was performed, we cannot unequivocally conclude that reproduction in the singles involved self-fertilization rather than parthenogenesis. Nor for that matter can we conclude that reproduction in pair-members was exclusively by cross-fertilization. However, several lines of indirect evidence tend strongly to rule out parthenogenesis as a possibility. First, while parthenogenesis has been reported as naturally occurring in several aquatic prosobranchs (Robson, 1923; Mattox, 1938; Warwick, 1952) and has been induced experimentally with various activating agents in bivalves (review by Raven, 1964), it is rare in pulmonates (Hyman, 1967; Grassé, 1968; Purchon, 1968). Bretschneider (1961) reported that 9% of the individuals of *Lymnaea stagnalis* he examined had oocytes that began developing parthenogenetically. Reports of parthenogenesis following interspecific mating in the laboratory (review in Grassé, 1968) are questionable, since self-fertilization was not ruled out. Second, Wille (1915) has interpreted the presence of a glandular sac at the junction of the tubular seminal vesicle and the hermaphroditic duct in *Rumina* as a specialized provision for self-fertilization. Third, parthenogenesis of the usual types occurring in animals would not cause a decrease in level of heterozygosity in populations (White, 1970), whereas selfing would. For these reasons, and because selfing is known to occur in a variety of pulmonates (reviews in Fretter & Graham, 1964; Grassé, 1968; Purchon, 1968), we conclude that the singles in our experiment reproduced by self-fertilization. We also assume that a significant, although unknown, portion of the reproduction of pair-members involved cross-fertilization. The genital apparatus in *Rumina* is in no way exceptional (apart from the modification of the seminal vesicle described by Wille, 1915), sperm are produced, and copulation is not infrequent (Batts, 1957; Arnaud, 1962; personal observation).

Although singles eventually achieved a reproductive performance at least equivalent to that of pair-members, laying commenced a little later on the average and full production of eggs was achieved much more gradually. This can be illustrated by comparing egg production per snail in the first month that laying occurred, that is from September 9 (when P1 first laid) through October 8. In this period, 57 of the 68 pairs laid, producing a total of 3379 eggs; thus 114 individual pair-members produced an average of 29.64 eggs each in this month. In contrast, 58 of the 105 singles laid in the same period, but a total of only 120 eggs was produced, or an average of 2.07 eggs per individual. Thus in this period egg production per individual was 14 times greater in individual pair-members than in singles. Moreover, individuals having the opportunity for cross-fertilization are capable of reaching full egg production 6 weeks before isolated individuals that must self-fertilize.

Several dozen young hatched from eggs laid by isolates were raised to maturity and are, at the time of this writing (February, 1972) laying their first small clutches of eggs. These second-generation isolates show no abnormalities in structure, growth rate, or behavior. If we are correct in supposing that *Rumina* populations in the Austin region are already fixed at all or the great majority of their loci, we do not anticipate any inbreeding depression as the experiment is continued through additional generations of selfing.

For pulmonate snails (especially aquatic species of the family Lymnaeidae), Hubendick (1951) suggested that apparent phenotypic uniformity within populations results in part from genetic homozygosity maintained by self-fertilization. But Hunter (1964) believed that self-fertilization is rare in natural populations, according to "existing field data." In point of fact, however, we know essentially nothing about the frequency of self-fertilization or of its consequences for genetic structure and phenotypic variability in natural populations. Elsewhere, we (Selander & Kaufman, 1973a) have outlined reasons for believing that selfing is in a large part responsible for the low levels of genic heterozygosity in *Rumina* populations both in North America and in Europe. Our findings for *Rumina* are also significant for genetic population biology in indicating that snail species can achieve extensive distributions and high population numbers in the apparent absence of genetic variation.

SUMMARY

Egg production and hatching success for individuals of the pulmonate snail *Rumina decollata* reared in isolation from the egg were equivalent to those for individuals reared in pairs. These results indicate that cross-fertilization is unnecessary for reproduction and, taken together with a previous report of a specialized modification of the seminal vesicle, point to selfing as an important mode of reproduction in the species. The unusual monogenic structure of *Rumina* populations in both North America and Europe is believed to be generated by a breeding system of facultative self-fertilization.

ACKNOWLEDGMENTS

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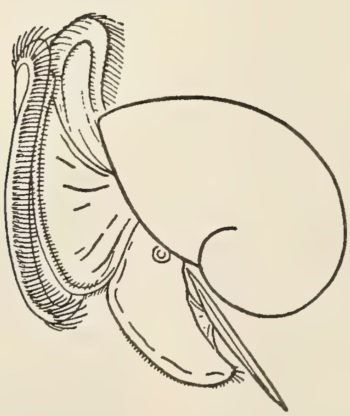

Spawning and Development of Some Columbellidae from the Caribbean Sea of Colombia (South America)

BY

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(15 Text figures)

INTRODUCTION

THE EGG CAPSULES OF THE COLUMBELLIDAE show a great variety of shapes as is evident from the descriptions of their spawn by THORSON (1940), BACCI (1942), FRANK (1941), KNUDSEN (1950), LEBOUR (1945), MARCUS & MARCUS (1962), SCHELTEMA (1963), and D'ASARO (1970). The spawn of 10 species of Columbellidae from Santa Marta (Colombia) also demonstrates this; 9 of these are described here for the first time.

This study was supported by the Deutsche Forschungsgemeinschaft, which made possible a stay of 18 months at the Instituto Colombo Aleman (ICAL) in Santa Marta, Colombia. Identification of the egg-laying females was accomplished with the aid of publications by WARMKE & ABBOTT (1961), MARCUS & MARCUS (1962), and KAUFMANN & GÖTTING (1970). Dr. R. Tucker Abbott verified the identifications on material sent to him.

METHODS

Spawn was collected in the sea near the ICAL with the help of fins, mask and snorkel, and in some cases with aqualung-diving equipment. Animals and spawn were collected from fall 1970 to spring 1972. Most egg cases described here were produced by animals held in aquaria with sea water running 12 hours a day. In some cases the way of capsule production could be observed on the glass and plastic walls of the aquaria. Freshly spawned egg masses were marked or taken out of the aquaria and then observed in glass dishes filled with sea water that was renewed every 2 days. The drawings of the capsules were made, immediately after spawning, by my wife with the aid of a binocular microscope. Capsular dimensions were determined on fresh oothecae containing living embryos. The spawn was observed in the laboratory of the ICAL at a room temperature of 25 - 27° C until the young hatched. The time for development in the glass dishes was more or less the same as that in the aquaria and in the sea.

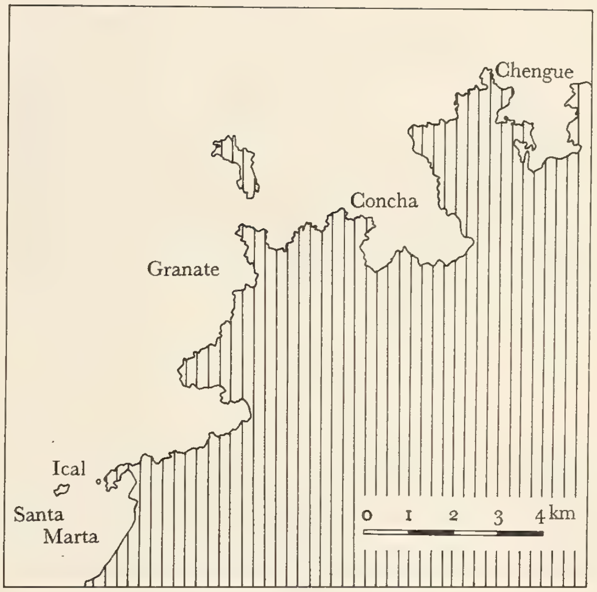


Figure 1

Map of the coast-line near Santa Marta, Colombia, showing the collecting stations for the individuals mentioned in this report.

LIVING PLACE IN THE SEA

Columbella mercatoria (Linnaeus, 1758) was found all around Santa Marta under coral rubble in water of 0 to 2 m depth in the reef zone, in the shallow lagoon behind it and in areas with extensive lawns of turtlegrass. Also commonly *C. mercatoria* was found on large bushes of *Sargassum* rooted near exposed rocky cliffs or coral reefs.

Anachis pulchella (Blainville, 1829) is restricted in its occurrence to lagoons behind coral reefs and was found attached to the underside of coral rubble behind reefs in Chengue Bay, north of Santa Marta, and also under flat stones in the extensive turtlegrass flats behind the coral reefs and thickets in this bay. Here, members of this species are the only representatives of the genus *Anachis*. In the reefstructure its occurrence overlaps that of *Anachis* sp.

Anachis sp. lives in depths from 0.2 to 1.5 m of water and is commonly found in all pebble and rubble zones where the rocks are overgrown by an algal crust. This species was found on and under stones near the Santa Marta airport, right below the ICAL, and in all bays north of Santa Marta up to Ensenada Arecifes. In areas, where rocks have a sandy bottom between them, *A. brasiliana* (v. Martens 1897) and *A. sparsa* (Reeve, 1859) join *A.* sp. in depths between 0.2 and 1.5 m of water. The latter sometimes can be found on *Sargassum* plants rooted in and just below the low water line together with *Nitidella laevigata* (Linnaeus, 1758), *N. nitida* (Lamarck, 1822), and *Mitrella argus* (Orbigny, 1842). *Nitidella laevigata* eats the leaves of *Sargassum* and clings so strongly to the plant that when the collector tears it off, the leaf is torn off also. If rocks and boulders are densely overgrown by algae just below the tidal zone, this species will also be found on them. *Nitidella nitida* mostly settles on the lower stems of *Sargassum* bushes close to the attachment to the rocky substrate. More commonly it is found on the underside of rocks between 0.1 and 1 m depth of water. It prefers rubble beaches without sand or mud between the rocks, where it lives in large groups. The activity of this animal generally takes place at night.

Mitrella argus (Orbigny, 1842) is not as common as the 2 species mentioned previously, but is regularly found under rocks in depths up to 1 m and on all parts of *Sargassum* plants where it eats small animals attached to the plant. Underneath pebbles and rocks in the zone between low water and 0.5 m depth of water *Mitrella ocellata* (Gmelin, 1791) is common, especially where no sand or mud is present between the rocks. In deeper water it is gradually replaced by *Nitidella nitida*.

Anachis obesa (C. B. Adams, 1845) feeds on hydroids and is found on the lower sides of rocks with hydroid colonies, on algae and turtle grass if they are used as substrates by hydroids. They can be found on hard objects lying on sandy or muddy bottoms; for example, on egg collars of naticids. *Anachis obesa* occurs in depths between 0.5 and 5 m of water.

LIFE IN AQUARIA

All 10 species have been kept in aquaria for some time, and, with the exception of *Anachis pulchella*, all have successfully been brought to copulation and spawning. *Co-*

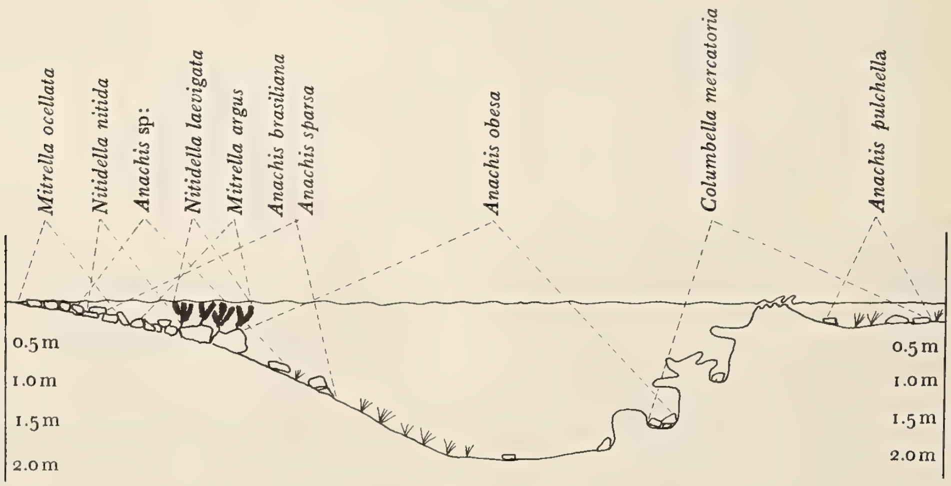


Figure 2

Generalized profile demonstrating typical habitats of 10 columbellid species of which the spawn is described. From left to right: rocky shore, rubble below low water, single large rocks with Sargassum-growth on them, turtle grass bottom, muddy to sandy bottom, coral reef, coral reef lagoon with turtle grass and coral rubble.

lumbella mercatoria can be fed with algae, especially with fine green filamentous ones; it also eats fish meat if near it, but does not go long ways to find it. *Nitidella laevigata* can be fed with *Sargassum* plants and will consume them completely with the exception of the stem and the larger veins in the leaves. It can grab leaves, holding them with the posterior part of its foot to the substrate and searching with quick motion with the anterior part of the foot for a new hold. *Nitidella laevigata* crawls some distance to eat flesh, extending its redbrown proboscis deep into it. *Mitrella argus* and *Anachis obesa* eat hydroids but also feed on fresh pieces of clam and fishmeat. All the others can easily be fed on fresh fishmeat. If fed well, all species can be held in great numbers in one aquarium with circulating sea water. *Mitrella argus, A. obesa,* and *N. nitida* have been observed reaching food through free water on their own mucus secreted by the foot. *Nitidella nitida* secretes mucus ribbons that are very durable, so that one ribbon, over 10 cm long, fixed to the shell of an individual making rapid escape motions, did not break.

EGG CAPSULES

Columbella mercatoria (Linnaeus, 1758)

(Figure 3)

In the Ensenada Granate north of Santa Marta, in water up to 1 m in depth, the egg capsules of *Columbella mercatoria* were found on stems and leaves of *Sargassum* plants which were also the habitat of the adults. In the Ensenada Chengue, capsules were also fixed to smooth spots on the underside of rocks in lagoons with lawns of turtlegrass behind reefs. In the bay of Santa Marta, spawn was found fixed to the shell of a living *Vasum muricatum* (Born, 1778) at Isla Moro.

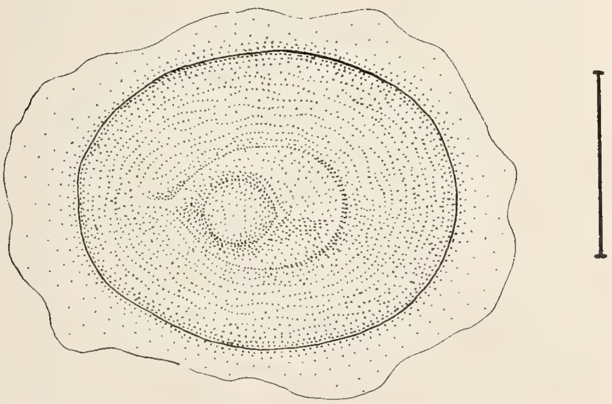


Figure 3

Ootheca of Columbella mercatoria seen from above (scale: 1 mm)

In the aquaria, the glass or plastic walls are usually used for oviposition. When fed well in aquaria, animals spawn at all times of the year, one female generally producing 2 to 6 capsules in one egg mass. Communal spawning was not observed. The capsules in one egg mass are attached individually to the substrate in loose groups to the aquarium panes, or in rows to *Sargassum* stems. The capsules are oval at the base, and the basal membrane extends in an irregular rim somewhat beyond the capsule walls. The cupola-shaped ootheca slopes to one side from the central escape aperture and from the other side more steeply from a projection on the apical plate. A suture divides the capsule in 2 halves. It crosses the opaque membrane of the escape aperture along its long axis, is enlarged into a ridge ending in the apical projection, and is only faintly discernible on the sides of the cupola. The sides of the ootheca have delicate transversal and radial wrinkles. The membrane of the escape aperture shows delicate transverse wrinkles. The opaque, translucent oothecae are 2 mm high, 3 mm long, and 2.5 mm wide. One capsule contains 16 to 27 green eggs that fill only $\frac{1}{4}$ of the lumen of the capsule. In development, 4 to 8 embryos devour all others and fill the entire lumen before hatching. After 33 days the membrane of the escape aperture dissolves and miniature snails crawl out.

Anachis pulchella (Blainville, 1829)

(Figure 4)

The spawn of *Anachis pulchella,* produced by freshly collected animals from the Ensenada Chengue, has only been found once (17th October 1971). The capsules were glued to the pane of the aquarium in a group of 6 without pattern in their arrangement. The ootheca is oval at the base, forming a cupola above an adhesion disk that extends beyond the capsule walls. The dome is divided into a lower and an upper part, separated from each other by one or a few concentric ridges. The lower part of the capsule is sculptured with a large number of radial wrinkles that end in the last $\frac{1}{3}$ of the rim of the adhesion disk at the lower part and at the lower edge of the concentric ridges at the upper part. The upper section of the capsule is characterized by a large escape aperture which is closed by an opaque membrane, in contrast to all other parts of the capsule, which are transparent and colorless. The long axis of the membrane of the escape aperture is followed by a suture that continues, reinforced by a ridge, down at

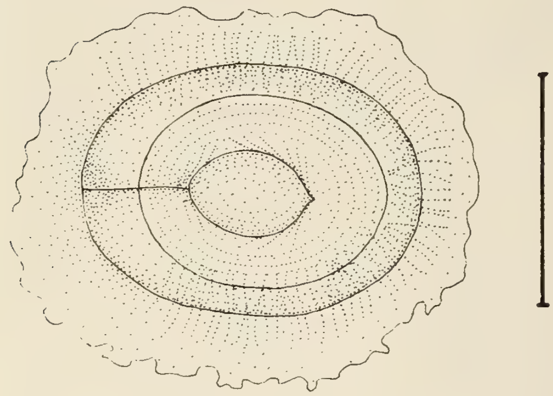


Figure 4

Ootheca of *Anachis pulchella* seen from above (scale: 1 mm)

one side of the capsule and is not visible on the other side in most oothecae. The membrane is delicately striped like a section of an onion, the stripes running into that point where the suture meets the rim of the escape aperture. From these points small wrinkles originate, crossing some of the weaker concentric ridges in the upper section of the capsule and ending there. The oothecae are about 2 mm long and 1.5 mm wide. They contain 2 to 9 (average 4) yellowish-white embryos at the beginning of their development which fill only very little of the lumen of the capsule. Later on the embryos fill the entire lumen. After 29 days of development the membrane of the escape aperture is dissolved and all embryos hatch as crawling miniature snails with a transparent shell showing 2 brown spots at the edge of the aperture and a brown line just above the sutural canal.

Anachis brasiliana (v. Martens, 1897)

(Figures 5A, 5B, 5C)

Anachis brasiliana attaches its spawn at all times of the year to hard substrates, wherever many adults can be found.

Animals, kept in aquaria, spawn if fed well. The capsules are glued to the glass and plastic panes of an aquarium in masses of 40 to 60 capsules by one female. Usually one spawning female attracts other females, so that large communal egg masses are produced. A single egg mass shows a pattern of orientation of the oothecae in rows exhibiting a hexagonal pattern if seen from above and a scaly pattern if viewed from below.

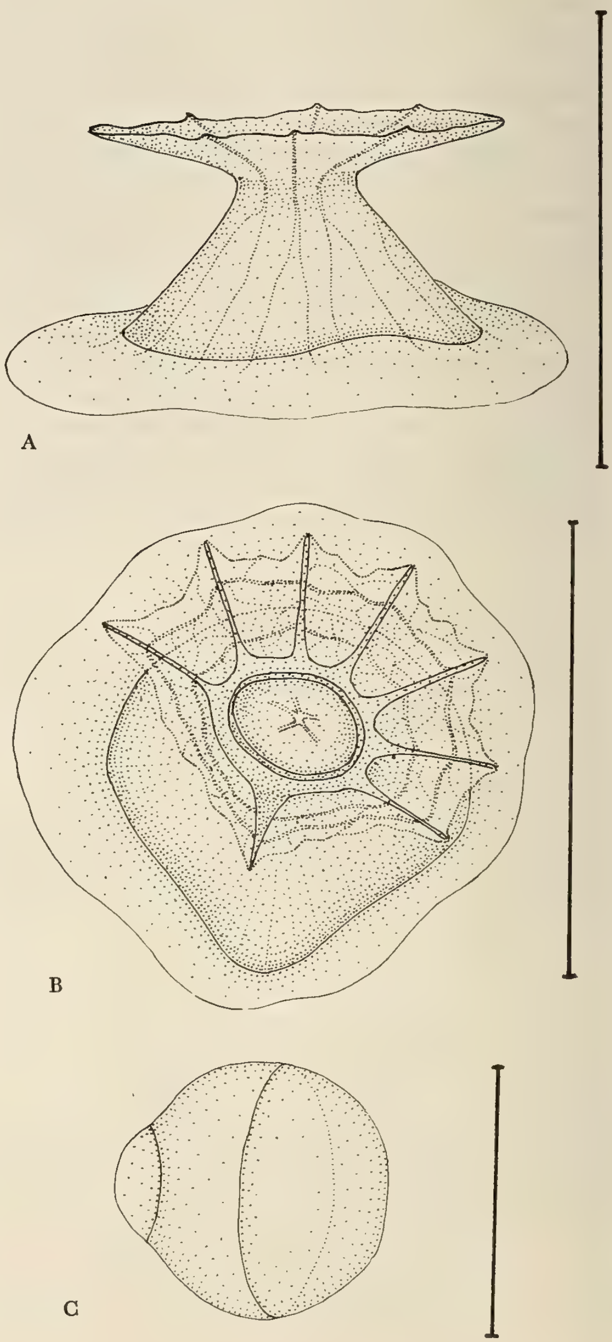


Figure 5

Ootheca of *Anachis brasiliana*

A: seen from the side; B: seen from above

C: before final shaping in the pedal gland (scale: 1 mm)

The mode of formation and attachment of capsules to the transparent panes of the aquaria was observed. To prepare for the later attachment of the entire egg mass, the female cleans the locality with her extended proboscis and bites off all kinds of growth from the substrate with her radula. After having cleaned an area sufficiently large, the female rests for some time, sitting without motion in one spot.

Then the first soft capsule is transported by ciliary movement in a fold to the frontal part of the foot's sole and is sucked here into the pedal gland. This still soft capsule, coming from the capsule gland, is spherical. It is divided into 2 halves by a suture separating one smooth hemisphere from another carrying a round escape aperture in its centre, which is closed by a convexly arching membrane.

After the capsule disappears into the pedal gland, the entrance to the gland is pressed against the spot of fixation of the capsule, and the capsule itself is milled and strongly moved about inside the gland for about 1 to 1½ minutes, until the disk of attachment becomes clearly visible. The female then rests, motionless, for 1 to 1½ minutes on the capsule. After 2 to 3 minutes the female leaves the now hardened capsule, shaped into its final form, by detaching the pedal gland from it and moving on with a searching motion of the frontal part of the foot. After about a minute of searching the female stops with opening of the pedal gland at the location for attachment of the next capsule. Then this capsule is passed from the oviduct to the pedal gland along a groove situated in the right anterior portion of the foot, formed temporarily for this purpose. The whole time needed for capsule formation amounts to about 4 minutes, so that the egg mass produced by one female requires about 3 to 4 hours. Fully formed capsules are fixed to the substrate with a flat round adhesion disk. One side of the disk is fixed in an arch to the substrate, the other side overlaps the capsular sides and the rims of the adhesion disks of the row of capsules produced earlier. This gives the scaly appearance of the egg mass seen from below (through the transparent panes of the aquarium). The walls of the capsule rise from the adhesion disk. They are supported by 16 ribs, 2 each joining at the upper part of the walls and continuing as 8 ribs, reinforcing a collar around the escape aperture. This collar has 2 unequal halves, one having 7 ribs and the other only 1. All collars in one egg mass point in the same direction so that the halves with the 7 supporting ribs point toward that part of the egg mass formed in the previous instance. The collar carries 2 concentric ridges connecting the stiffening ribs with each other. The lid of the escape aperture bears a 5- to 7-rayed fold in its centre. Each transparent ootheca, 0.7 - 0.8 mm wide and 0.4 - 0.5 mm high, contains 4 to 15 embryos (average 10). After 11 to 13 days the white eggs have developed into veligers with a simple velum and a transparent shell with a brownish siphonal canal; they hatch through the open escape aperture after dissolution of the membrane.

Anachis sparsa (Reeve, 1859)

(Figure 6)

Anachis sparsa spawn was found at different times of the year on the underside of rocks in about 50 cm of water below the stairs near the pumping station of the ICAL. Sometimes capsules were found fixed to the leaves of *Sargassum* plants rooted on the rocks.

A well fed population of *Anachis sparsa* copulates and spawns at all times of the year in the aquaria. One female produces up to 60 capsules in one egg mass on the glass or plastic walls of the aquaria. Usually a spawning female attracts other females, as well as males, of the same species. The males copulate with spawning and non-spawning females. The newly arrived females also begin producing egg masses, so that at one time large patches of egg masses are produced at different spots in the aquarium, containing many hundreds of capsules. The capsules are arranged in irregular rows, and the rims of the adhesion disks usually fuse with each other. The walls of the cone-shaped capsule rise from the round adhesion disk and end in a projecting edge, forming a collar around the concave mem-

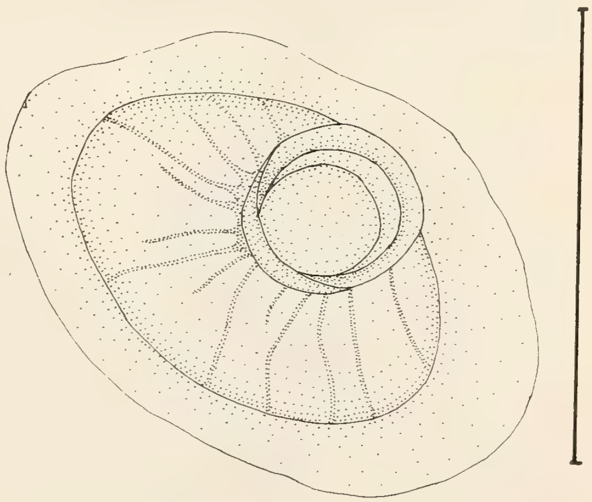


Figure 6

Ootheca of *Anachis sparsa* seen from above (scale: 1 mm)

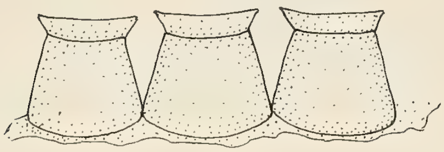
brane of the escape aperture. The collar is a little inclined in relation to the plane of the adhesion disk so that all collars of one honeycomb-shaped egg mass point in the same direction. The sides of the capsules are re-inforced by 20 to 25 somewhat irregular radial ridges. The transparent, colorless oothecae measure about 1 mm in diameter, if more ovoid 1.2×1 mm, and are 1 mm high. The 10 to 25 (average 17) embryos lie loosely on the bottom of the lumen of the capsule at the beginning of development and later fill the entire interior. At first they are white; at hatching, after 11 to 13 days of development, they are veligers with a large two-lobed rectangular velum and a transparent shell with a brown siphonal canal. The small foot carries an operculum that cannot close the aperture.

Anachis obesa (C. B. Adams, 1845)

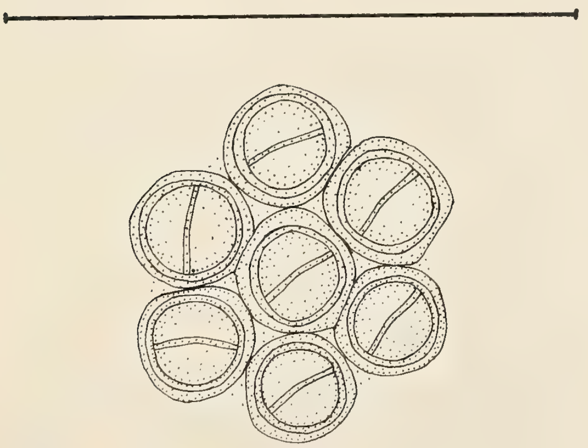
(Figures 7A, 7B)

In the sea, capsules of *Anachis obesa* have only been found on the stalks of hydroids, arranged in a row of one capsule behind the other. Well fed animals produce at all times of the year large communal egg masses fixed to the walls of the aquarium. One female secretes between 45 and 100 capsules in one egg mass, but communal egg masses sometimes contain more than 1000 capsules. Usually one spawning female induces spawning in other females so that up to 8 females may be observed spawning at the same time, adding to the communal egg mass.

The capsules in one egg mass are arranged close to each other so that the basal membranes of all capsules are fused to each other with their rims. The bases of the cone-shaped oothecae are often touching and deforming each other, thus producing a hexagonal pattern of the egg mass if viewed from above. The weakly conical cylinders end in a short collar surrounding the escape aperture. The membrane of the escape aperture is crossed by a lamellar transverse ridge. The transparent, colorless capsules measure only 0.2 - 0.25 mm in diameter and height, and each capsule contains only one embryo. After 6 days of development the white egg, with much space in the lumen of the capsule, has grown into a transparent veliger filling the whole capsule. At hatching, the edge of the round lid of the escape aperture dissolves and the lid is turned into a vertical position, with the median ridge acting as a hinge. The hatching veliger has a round, bilobed velum and a transparent shell with a yellowish-brown tint at the edge of the aperture.



A



B

Figure 7

Ootheca of *Anachis obesa*

A: seen from the side; B: seen from above (scale: 1 mm)

Anachis sp.

(Figure 8)

Spawn of *Anachis* sp. is found at all seasons of the year at the localities where adults of this species are common. The capsules are fixed to the underside of rocks, rarely to leaves of *Sargassum* plants rooted on the rocks. Well fed animals spawn at all times of the year, fixing the capsules to the glass or plastic walls of the aquaria.

The rectangular, brick-shaped oothecae are arranged in a row consisting of from 2 to 11 capsules, with an average of 4 capsules. The longer sides of the oothecae in a row are fused with each other and slope vertically at the end of the adhesion membrane. The upper plate of the rectangular capsule is surrounded by a ridge that extends out into a plate overlapping the next capsule at one of the corners. These projections of the rim from the apical plate point in the same direction in one row of capsules. An escape aperture is not present. The whole upper plate is covered by a tegmentum made of tubercles, bristles and ridges. At hatching a roundish hole somewhere in the apical plate opens due to dissolution originating from the interior of the capsule. No chewing activities of the developing larvae from the inside at the apical plate can be observed. The opaque capsules are 1.5 mm long, 1 mm

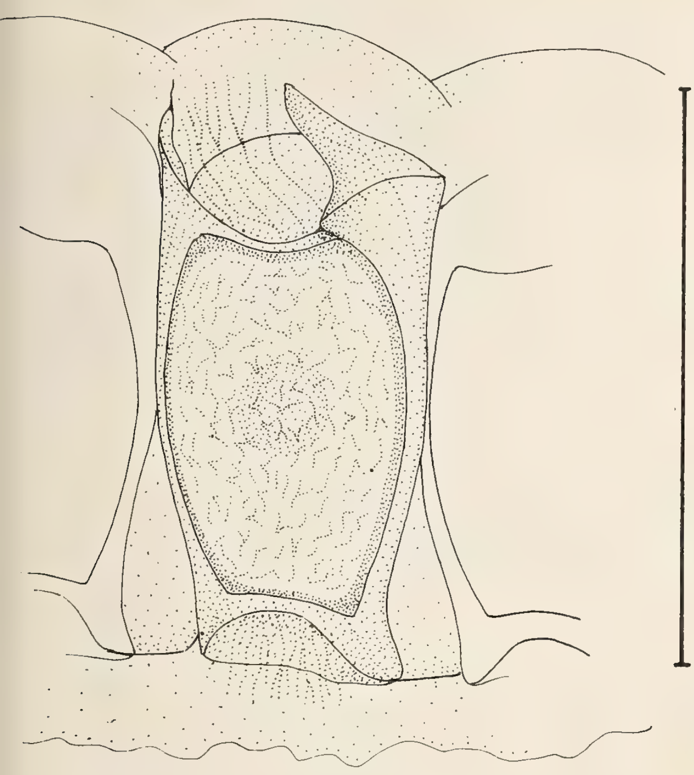


Figure 8

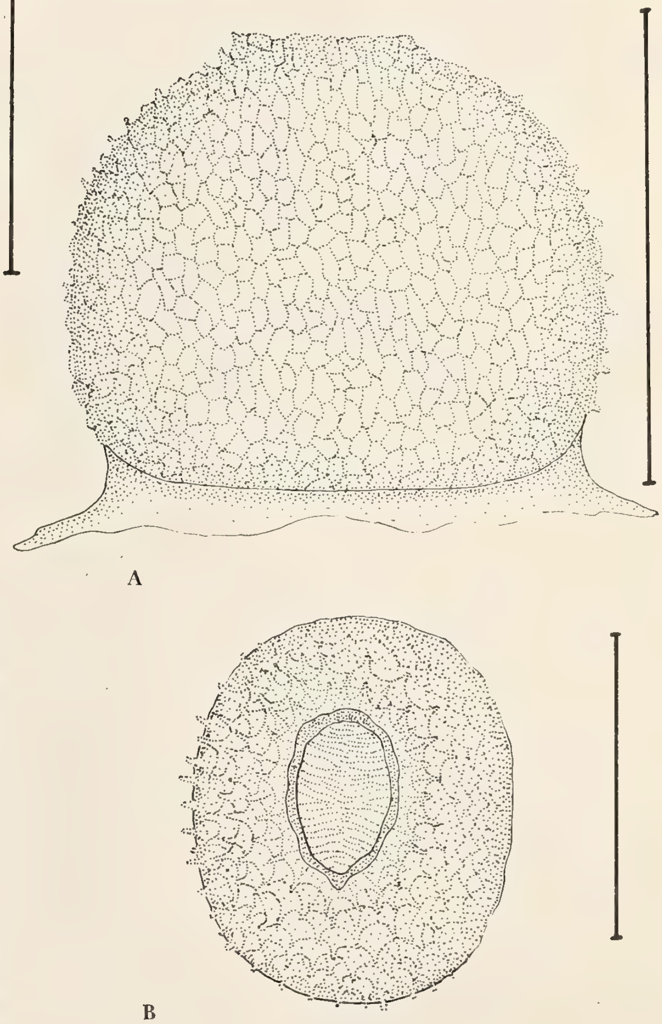
Ootheca of *Anachis* sp. seen from above (scale: 1 mm)

wide and 0.7 mm high. Each capsule contains one, rarely 2 white eggs filling only a small portion of the lumen. In later stages of development, the embryo fills much of the interior. After 26 days of development a fully differentiated little snail with a transparent, light brown shell crawls through the irregular dissolution hole of the apical plate.

Nitidella nitida (Lamarck, 1822)

(Figures 9A, 9B)

Fixed to the lower part of *Sargassum* plants rooted on the rocks just below low water level, below the ICAL, capsules produced by *Nitidella nitida* are common on stems and leaves. Spawn can also be found at all times of the year on the underside of rocks in areas where adults of this species are common. Sometimes as many as 58 capsules of different ages can be found in communal egg masses. In the aquarium, egg masses of one female, consisting of 3 to 8 capsules, are fixed to the glass and plastic walls and to the inside of plastic hoses. Usually the capsules of one egg mass are not arranged in a specific pattern, but mostly in groups and rows of 2 or 3 capsules close together so that the basal membranes of neighbors are fused at the rim. The capsules are flask-shaped and oval or round in cross section at the base. The round adhesion disk is smooth and transparent. The opaque sides of the capsule are covered with a reticular pattern of ridges, which at the crossing points of the ridges are drawn out into vertical small pointed projections. The oval escape aperture is closed by a transparent membrane that is sculptured with a large number of very fine transverse wrinkles. The



A

B

Figure 9

Ootheca of *Nitidella nitida*

A: seen from the side; B: seen from above (scale: 1 mm)

capsules measure 1.25 mm in diameter and are of about the same height. Each capsule contains 6 to 10 white embryos with much free space in the interior at first. After 29 to 30 days of development the embryos, now completely filling the lumen of the capsule, are ready to hatch. The membrane of the escape aperture dissolves completely and miniature, fully developed snails with yellowish-white body and opaque shell crawl out.

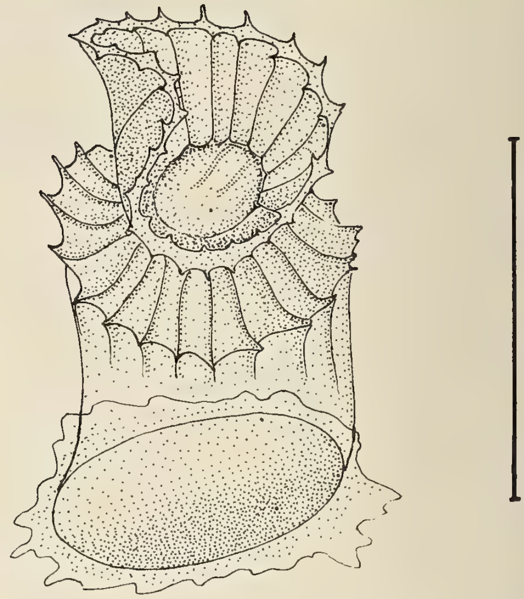
Nitidella laevigata (Linnaeus, 1758)

(Figures 10A, 10B)

Nitidella laevigata spawn was found at all times of the year on *Sargassum* plants growing on rocks below the ICAL. Usually the leaves of *Sargassum* were used for affixing the capsules, rarely the stem or other thallous algae. Occasionally egg masses were found on the undersides of rocks just below low water level at the ICAL and behind a small *Porites* reef in a few decimeters of water in the bay of Villa Concha.

Animals kept in aquaria usually produce spawn only shortly after collection in the sea and rarely after longer times of life in the aquarium. Spawn is then fixed to *Sargassum* leaves and, if none are available, to the walls of the aquarium. Spawn of one female consists of 3 to 26 capsules (average 12). Communal spawning of more than 1 female at one time has never been observed. The capsules are always arranged in rows of 2 or 3 lines in such a way that the capsules of the second line are fixed beside the interstices of the first line. The collars surrounding the escape aperture are all bent into the same direction in one egg mass. The rims of the basal membranes of the capsules in one egg mass are fused to each other. Usually one egg mass covers most of the upper or lower surface of one *Sargassum* leaf and egg masses fixed to other substrates reflect the size and shape of a *Sargassum* leaf.

The cylindrical capsule is fixed to the smooth, transparent basal membrane at an angle, varying from capsule to capsule, and most strongly inclined at the edges of the egg mass. The apical plate forms a sharp edge with the sides of the capsule, and ridges crossing it are drawn out into projections. The round escape aperture lies in the middle of the apical plate and is closed by a transparent membrane. The membrane is sculptured with rows of 5 to 8 furrows. The escape aperture is surrounded by a high collar which is bent on one side toward the escape aperture and on the other side away from it. The collar is supported by 25 to 30 ribs which continue across the apical plate and over the edge down to the middle of the side walls of the capsule. Each rib ends in 2 points at the edge of the collar, one pointing toward the inside and the other toward the outside of the collar.



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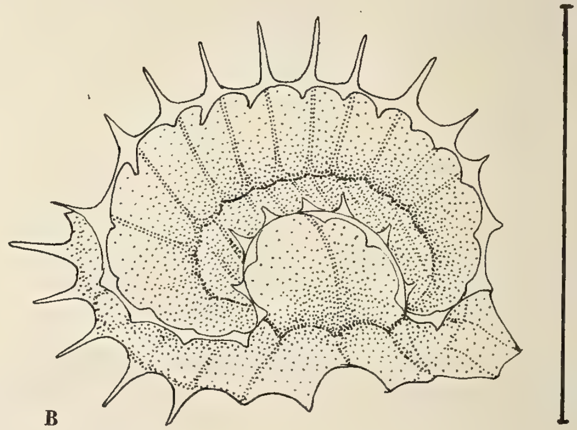

B

Figure 10

Ootheca of *Nitidella laevigata*
A: seen from the side; B: seen from above (scale: 1 mm)

Each opaque capsule contains between 15 and 30 white embryos with much empty space in the lumen immediately after secretion. After 13 days the membrane of the escape aperture dissolves, setting free veligers with a rounded 2-lobed velum, a transparent shell with a brownish siphonal canal, and a small operculum that cannot close the aperture.

Mitrella ocellata (Gmelin, 1791)

(Figures 11A, 11B)

Capsules can be found, attached to the undersides of rocks in the areas where *Mitrella ocellata* adults are common, at all times of the year. The lower parts of *Sargassum* plants rooted on rocks near low water level are often used for oviposition.

In the aquarium, spawning females usually prefer empty clam shells to the aquarium walls. One egg mass contains 1 to 6 irregularly arranged capsules, only rarely fixed to the substrate so close to each other that the disks of attachment are fused with one another at the rim. The irregular oval basal membrane extends only in a narrow rim beyond the capsule walls. The smooth capsule is dome-shaped, one side sloping more rapidly than the other. The large oval escape aperture is closed with a transparent membrane and surrounded by a smooth lamellar collar. The escape aperture is somewhat shifted from the centre of the capsule cupola along the long axis toward the strongly sloping side. The collar continues on the more gently sloping side, almost down to the base of the capsule and is here higher than at the upper side, at the edge of the escape aperture. The whitish opaque capsule is up to 1.5 mm long, 0.8 mm wide, and 0.7 mm high. Capsules contain 11 to 27 white embryos (average 17) and there is much space in the lumen when the capsules are freshly secreted. All embryos undergo development and hatch after 13 to 14 days as veligers, showing a 2-lobed round velum, a transparent shell with a brown siphonal canal, and an operculum that cannot close the aperture.

Mitrella argus (Orbigny, 1842)

(Figure 12)

Single capsules of *Mitrella argus* can be found at all times of the year glued to leaves of *Sargassum* plants rooted on rocks at the ICAL just below the intertidal zone. In the aquarium capsules are produced when the animals are fed well. Only single capsules are fixed to the leaves of *Sargassum* or to the plastic panes. The egg masses sometimes consist of loose groups of capsules with no pat-

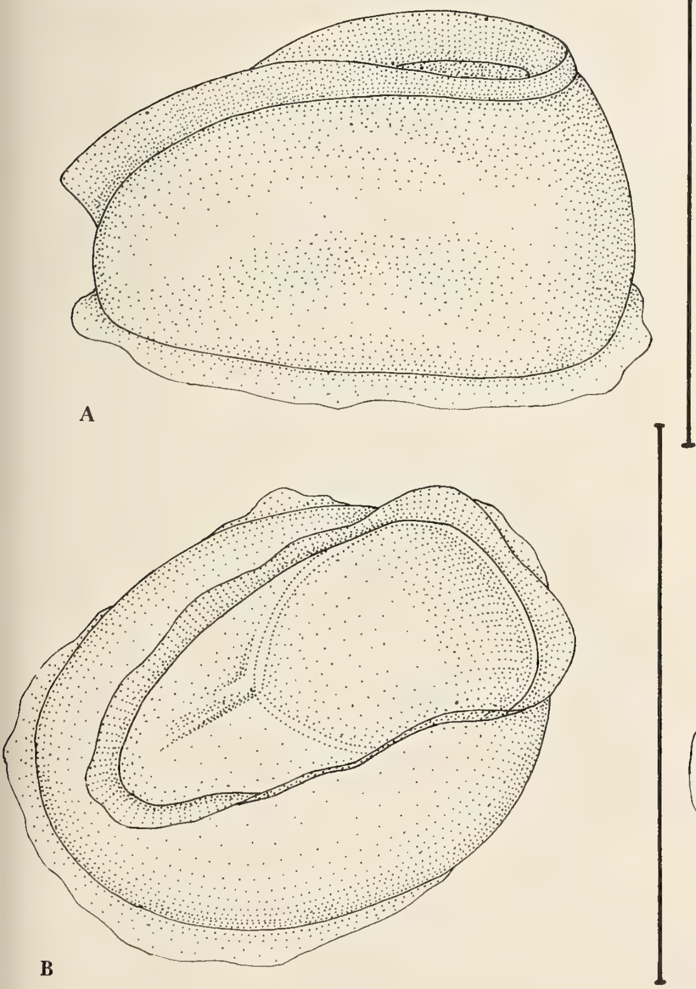

Figure 11

Ootheca of *Mitrella ocellata*

A: seen from the side; B: seen from above (scale: 1 mm)

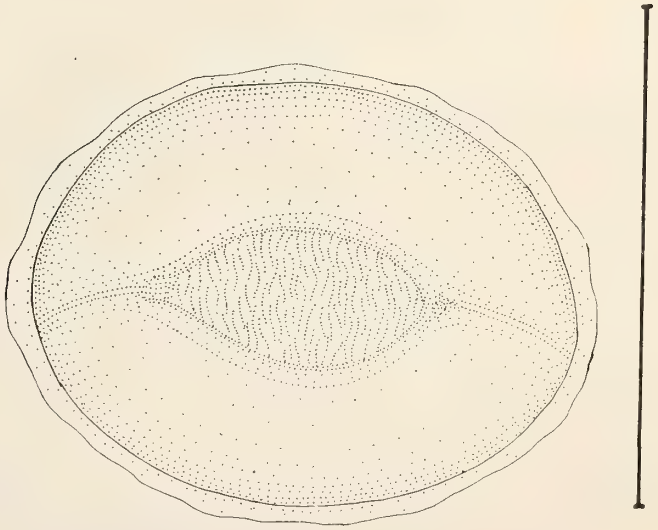

Figure 12

Ootheca of *Mitrella argus* seen from above (scale: 1 mm)

tern of arrangement and with different stages of embryonic development.

The capsules have the shape of a shallow dome on a broad, irregularly rounded disk of adhesion which only extends in a narrow rim beyond the capsule walls. The walls are smooth and in the cupola a large spindle-shaped escape aperture is situated, closed by a clear membrane with delicate transverse furrows. From the pointed sides of the escape aperture, ridges run down the sides of the capsule to the basal membrane. The ootheca measures about 1 mm in diameter, is about 0.25 mm high and contains 12 to 16 white eggs which occupy only a small fraction of the lumen of the capsule at the beginning of their development. Later, the embryos fill the entire lumen of the capsule and are freed after more than 6 days of development by dissolution of the membrane of the escape aperture. The hatching veliger has a simple rounded 2-lobed velum and a transparent shell with a reddish-brown siphonal canal.

DISCUSSION

According to the literature and my own material 6 morphological groups of columbellid egg capsules can be distinguished.

1. Group of *Mitrella argus*

The simplest shape of egg capsules is found in *Mitrella argus,* resembling the unformed soft capsules leaving the capsule gland. The transformation consists only of hardening the membranes and fixation to the substrate with the aid of a round adhesion disk by the pedal gland. Similar capsules are widely observed in other families of Neogastropoda but have so far not been described from Columbellidae. Egg cases of members of the genera *Bedevina* (Amio, 1963), *Trophon* (Thorson, 1940, 1946), *Risomurex* and *Drupa* (own observations) in the family Muricidae, *Fusus* (Fioroni & Portmann, 1968) in the family Buccinidae, *Tritia* (Amio, 1963) in the family Nassariidae, *Mitra* (Franc, 1942), *Pusia* (own observations) in the family Mitridae, and *Drillia, Bela* and *Philbertia* (Thorson, 1946) in the family Turridae are of the same general shape.

2. Group of *Anachis sparsa*

The next, more complicated shape of columbellid capsules is characterized by a collar surrounding the escape aperture. This collar may be smooth and simple and the capsules unsculptured as in *Anachis sparsa, A. avara* (Say, 1822) (Scheltema, 1969), and here all embryos develop

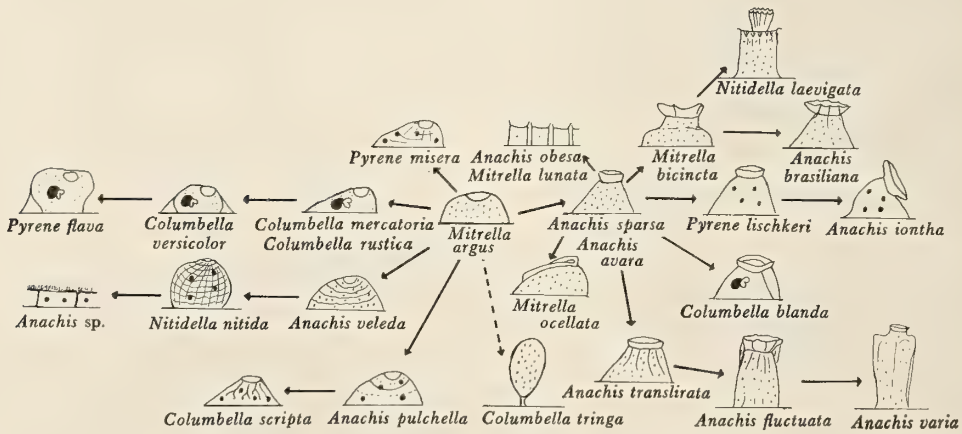

Figure 13

Diagram showing hypothetical links between capsules of different shapes and with different embryonic development within the columbellids. Capsules with small dots represent those with veligers hatching, capsules with large dots those with all embryos hatching as small crawling snails, and capsules with one big embryo and many small dots represent directly developing embryos consuming nurse eggs.

and hatch as veliger larvae. The same general shape of capsules is observed in *Anachis translirata* (Ravenel, 1861) (SCHELTEMA, *op. cit.*), *A. fluctuata* (Sowerby, 1832) and *A. varia* (Sowerby, 1832) (D'ASARO, 1970). Here also all eggs develop into veliger larvae, but the capsules are laterally sculptured by wrinkles and ridges and the capsules of the latter 2 species are more columnar than those of the others.

Simple capsules with large collars around the escape aperture are produced by *Pyrene lischkei* (Smith, 1879) (AMIO, 1963) and *Anachis iontha* (Ravenel, 1861) (PERRY & SCHWENGEL, 1955). But here the young hatch as crawling miniature snails without having fed on nurse eggs.

Similar capsules are figured and described as unidentified spawn by LEBOUR (1945) from Bermuda. The capsules were attached to hydroid stems (LEBOUR, *op. cit.*, text fig. 33) and related to *Columbella*; larval development is direct. *Columbella blanda* (Sowerby, 1844) (THORSON, 1940) differs from the last described capsule shapes in having nurse eggs.

The small columbellids *Anachis obesa* and *Mitrella lunata* (Say, 1826) (MARCUS & MARCUS, 1962) produce large egg masses with small capsules each containing only one egg that develops into a planktotrophic veliger larva.

The collar surrounding the escape aperture of *Mitrella ocellata* extends almost to the base of the sides of the capsule with one of its ends and is farther down on the side. Here the eggs develop into veliger larvae.

Mitrella bicincta (Gould, 1860) (AMIO, 1963), *Anachis brasiliana,* and *Nitidella laevigata* capsules are characterized by a more complexly shaped collar around the escape aperture. The oothecae of *A. brasiliana* from Santa Marta show close relationship to oothecae of this species from Brazil, as described and figured by MARCUS & MARCUS, 1962. The Brazilian capsules show a collar with radial symmetry and 10 stiffening ribs, while the capsules from Santa Marta have only 8 stiffening ribs arranged in a bilaterally symmetrical collar. Also the number of capsules in Brazilian egg masses is (with 10) much lower than that of the Colombian with up to 60 capsules shed by one female.

3. Group of *Columbella mercatoria*

In this group dome shaped capsules are combined with an asymmetrically located escape aperture. *Pyrene misera* (Sowerby, 1844) (AMIO, 1963) produces egg masses which hold eggs developing into crawling miniature snails before hatching without feeding on nurse eggs. All other members of this group have nurse eggs. *Columbella mercatoria* and *C. rustica* (Linnaeus, 1758) (FRANC, 1941) (own observations) have bilaterally symmetrical capsules, while those of *C. versicolor* (Sowerby, 1832) and *Pyrene flava* (Bruguière) (PETIT & RISBEC, 1929) become more irregular.

4. Group of *Nitidella nitida*

Egg capsules with radial symmetry and sculptured sides are produced by *Nitidella nitida, Anachis pulchella, A. veleda* (Duclos, 1846) (MARCUS & MARCUS, 1962) and *Columbella scripta* (Linnaeus, 1758) (THORSON, 1940). The sculpture of the sides is radial in *C. scripta* and concentric in *A. veleda* and *A. pulchella. Nitidella nitida* has both directions in the sculpture, producing ridges and at the crosspoints additional spines. Only *A. veleda* has veliger larvae hatching; all others produce eggs from which young miniature snails hatch without feeding on nurse eggs in the capsule.

5. Group of *Anachis* sp.

Rows of brick-shaped egg capsules of *Anachis* sp. are the only representatives of this group. Here only 1 or 2 embryos in each capsule undergo direct development.

6. Group of *Columbella tringa*

Capsules of *Columbella tringa* (Laurent) (PETIT & RISBEC, 1929, fig. 4) are of oval shape, standing on a peduncle.

Description of *Anachis* sp.

(Figures 14 and 15)

Shell: Height up to 10mm, width 3.7mm, total of whorls 8, protoconch $2\frac{1}{2}$ - 3 whorls, smooth. Junction of protoconch with teleoconch indistinct. Teleoconch with distinct ribs, strongest near body whorl. Body whorl with 12 - 13 rounded ribs as broad as their interspaces. Suture smooth or undulated by tips of ribs. Spiral cords strong and crossing ribs. Distinct cord on penultimate whorl (5), body whorl (8 - 10) and basal ones (10) on the anteriormost part of body whorl. Aperture medium wide, sigma shaped. Interior of outer lip with 6 - 8 denticles, the first 3 (adapical ones) thickest. Interior of inner lip with 4 - 5 strong teeth. Columellar callus raised into a smooth little lip at its edge. Periostracum thin, transparent, on living specimens often polished off. Color of dry shell variable from light orange, dark purplish brown to black. Living snails show more dull brownish to black colors. Some specimens uniformly colored, others variegated with white.

Operculum: Light yellow, translucent, concentric, rounded in front and pointed behind, broadest behind

Figure 14

Shell of *Anachis* sp. (scale: 1 mm)

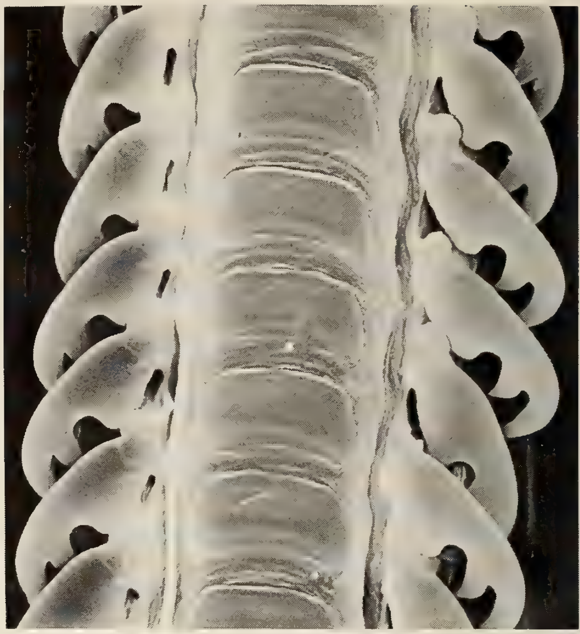

Figure 15

Radula of *Anachis* sp. (magnification × 660)

its middle. Nucleus terminal, projecting very slightly beyond opercular lobe. From the nucleus a broadening cord curves to the rounded side, perpendicular to the growth lines. Operculum up to 1 mm long, with up to 8 thick growth lines, with about 8 thin lines between each 2 of them.

Soft Parts: Siphon opaque with white and brown spots; proboscis, head-foot irregularly striped and dotted with black and dark brown; sole of foot yellowish opaque with white spots at the rim; large eyes at the base of the tentacles; tentacles opaque with internal white spots and 2 black to dark brown external rings.

Radula: Central tooth plate broad, rounded at the edges; lateral teeth with 3 cusps, the first broad and rounded, the second and third narrow and pointed.

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Some New Gastropod Representatives from the Brackish Waters of the Adriatic and Aegean Seasides

BY

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(2 Plates; 3 Text figures)

THE COASTAL REGION along the Yugoslav part of the Adriatic Sea is relatively narrow, separated from the continental part of the Balkan Peninsula by the high mountain chain of the Dinarides. Yet in this narrow zone a number of rather large rivers with relatively long courses has been formed. The extreme lower courses of these rivers contain brackish water, and around the mouth of each of them a more or less extensive brackish zone exists, depending upon the quantity of fresh water in the river and upon some other factors.

A specific fauna inhabits these brackish waters. When the brackish water gastropods from this area are considered, one usually mentions several species of the genus *Hydrobia,* which subject I will discuss on another occasion. This time I wish to describe two new brackish water genera with five species, about whose representatives I could not find any data in the malacological literature. I suppose that previous investigators, who studied the malacological material from these waters, probably considered these species members of the above mentioned genus.

Semisalsa Radoman, gen. nov.

Shell conical, elongated, with moderately pointed apex, in younger specimens smooth, shining and transparent; moderately tumid whorls, separated by a rather deep suture, gradually and regularly expanding in width. Aperture usually angular at the top, in rare specimens slightly round (at the top), but very narrow. The margins of the aperture thin, peristome discontinuous, with columellar margin applied to the last whorl so that this margin often is seen as a callus; outer lip gently curved, umbilicus closed, in rare cases (in the same species) barely slitlike.

Central tooth of the radula with 2 to 4 basal cusps. Stomach without a caecal tube-shaped appendix on its anterior, oesophageal end (Figures 3A and 3B), characteristic for the genus *Hydrobia.*

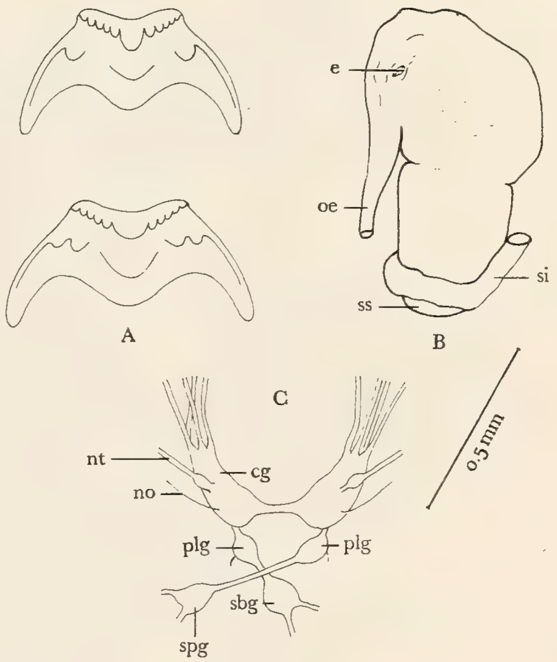

Figure 3

Semisalsa dalmatica Radoman, spec. nov.

A: Central tooth of radula; B: Stomach; C: Nervous system
cg – cerebral ganglion e – entrance of the duct from the digestive gland ("liver") no – nervus opticus oe – oesophagus plg – pleural ganglion sbg – subintestinal ganglion si – small intestine spg – supraintestinal ganglion ss – style sac

Nervous system (Figure 3C) with a relatively long cerebral commissure, clearly perceptible cerebro-pleural connectives, long pleuro-supraintestinal and shortened but clearly differentiated pleuro-subintestinal connective; a ganglionic thickening is present on the tentacle nerve and absent from the lateral pedal nerve; pro- and meta-podial ganglia moderately developed.

Female reproductive system (Figures 4B and 4C) is very characteristic: a small, pin-shaped genital chamber with a long duct is present and, also with a long duct, only 1 seminal receptacle, applied to the genital chamber. The oviduct in a "loop" is widened, making 2 to 3 whorls, and continues in a short terminal part penetrating into the accessory gland by which this genus is essentially differentiated from the genera *Hydrobia, Pyrgula* and their relatives (Radoman, 1955). The female accessory gland, terminating at the genital pore, exhibits 4 colour nuances, which means that this gland is constituted of 4 parts, which broadly communicate with each other: the first is whitish, the second "glassy" ("colourless"), the third shows the most expressive character of the genus – in the fresh state it is the colour of "terracotta" and in material

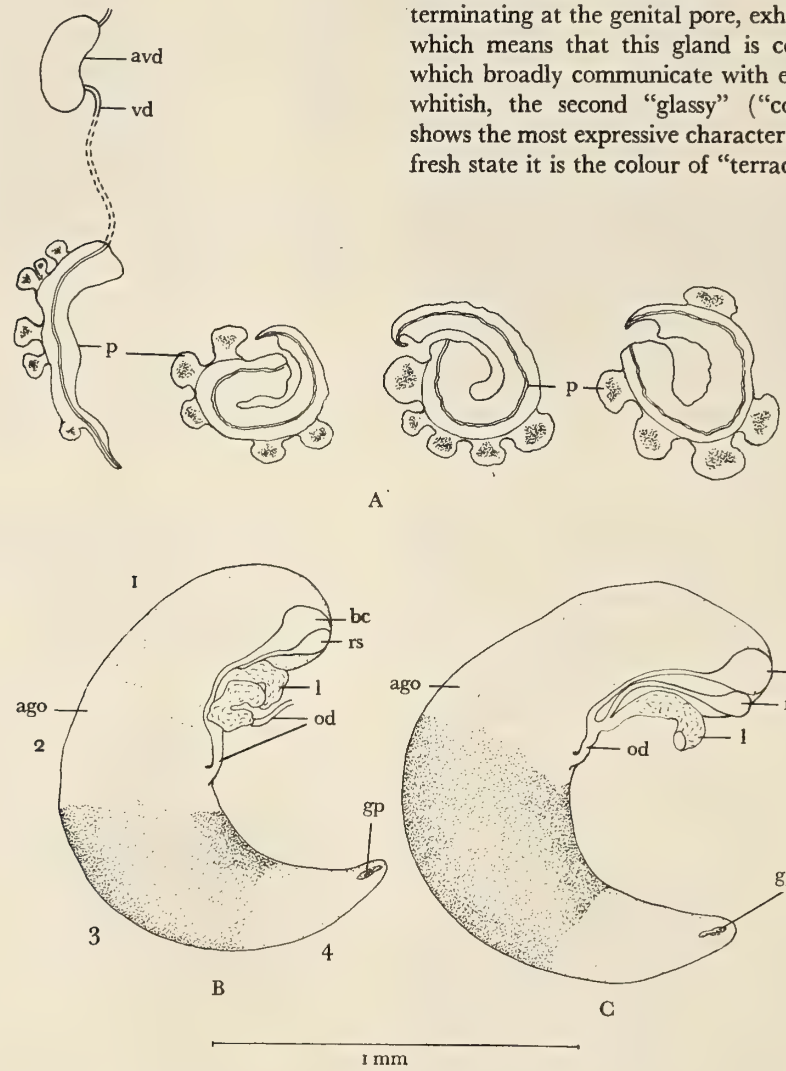

Figure 4

Semisalsa dalmatica Radoman, spec. nov.

A: Male reproductive system (without seminal gland); B: Female reproductive system (without ovary) in natural position, showing 4 colour nuances. 1 – whitish; 2 – "glassy"; 3 – "terracotta"; 4 – white

C: the same parts partially dissected: ago - accessory gland of oviduct avd - accessory gland of vas deferens bc - bursa copulatrix gp - gonopore l - loop of oviduct od - oviduct p - penis rs - receptaculum seminis vd – vas deferens

preserved in alcohol for a long time, this colour changes to reddish-yellowish (Figures 4B and 4C). Due to this colouring this relatively big gland can be observed through the transparent shell and on that basis the females can be separated from the males. The terminal, fourth part of the accessory gland is white.

The male accessory gland is small (Figure 4A). The penis is very characteristic (Figure 4A): it is elongated, with a pointed end and with 5 outgrowths on the right side (the second one sometimes is double).

Type species: *Semisalsa dalmatica* Radoman, spec. nov.

Etymology: the name of the genus is derived from the brackish water (semi-salsus = semi-salt) in which all representatives of this genus, known up to now, live.

I have found 3 species of this genus which will be here briefly comparatively described.

Semisalsa dalmatica Radoman, spec. nov.

Shell (Figure *1*A), in relation to that of other species, mostly elongated and slenderest, with a few more whorls (see Table 1).

Measurements: in Table 1

Type Locality: brackish water spring Pirovac, near the small town of the same name, by the main road Zadar-Šbenik, Yugoslavia; in addition to Pirovac spring also found in lower brackish course of the Zrmanja river, near the town Obrovac, and in the brackish Cetina river, 2 to 3 km from the town Omiš, also in Yugoslavia.

Holotype: Prirodnjački Muzej, Beograd (PMB, Museum of Natural History, Beograd) 7997/1; collected in July 1972 by Pavle Radoman

Paratypes: PMB 7997/2 (4); same data as for the holotype

Semisalsa rausiana Radoman, spec. nov.

This is the smallest of the 3 species, its shell (Figure *1*B) having the smallest number of whorls and its aperture, in proportion to the shell length, being the highest one.

Measurements: in Table 1

Type Locality: brackish part of Rijeka dubrovačka (Dubrovnik River) near Dubrovnik, Yugoslavia.

Etymology: this species is named after the old Roman name of Dubrovnik – Rausium.

Holotype: Prirodnjački Muzej, Beograd (PMB) 7998/1; collected in July 1968 by Pavle Radoman

Paratypes: PMB 7998/2 (3); same data as for the holotype

Semisalsa graeca Radoman, spec. nov.

The height of the shell (Figure *1*C) is nearly the same as in the type species, yet on the average somewhat smaller, with fewer whorls, proportionately larger, with relatively higher aperture (in proportion to the shell length) than in the type species.

Measurements: in Table 1

Type Locality: brackish water spring Tramana (?or Tratana), near the town of the same name, close to the main road Larissa-Athens, about 120 km north of Athens, Greece.

Holotype: Prirodnjački Muzej, Beograd (PMB) 7999/1; collected in July 1964 by Pavle Radoman

Paratypes: PMB 7999/2 (3); same data as for the holotype

Table 1

	shell		aperture		number
	length	width	length	width	of whorls
Semisalsa dalmatica	3.2 - 4.4	1.6 - 1.9	1.2 - 1.5	0.9 - 1.2	$5\frac{1}{2}$ - $6\frac{1}{4}$
Semisalsa rausiana	2.6 - 3.1	1.3 - 1.6	1.1 - 1.2	0.8 - 0.9	$4\frac{3}{4}$ - 5
Semisalsa graeca	3.1 - 4.2	1.6 - 2.1	1.2 - 1.6	1.0 - 1.2	$5\frac{1}{4}$ - 6

Obrovia Radoman, gen. nov.

Shell conical, with moderately pointed apex; moderately tumid whorls, separated by a rather deep suture, regularly expanding in width. Aperture egg-shaped, narrowed, almost angular at the top. The margins of the aperture rather thickened, especially the columellar one; outer lip vertical, peristome continuous. Umbilicus slit-like.

Central tooth of the radula with 2 basal cusps, and each tooth, except to a certain extent the second marginal one, provided with a small number of little teeth. Stomach with a caecal tube-shaped appendix on the oesophageal end (Figure 5).

The nervous system as in *Hydrobia*: long pleuro-supraintestinal and very shortened pleuro-subintestinal connective, so that these latter 2 ganglia are almost grown together; a ganglionic thickening present on the tentacle nerve, absent from the lateral pedal nerve.

The accessory part of the female reproductive system is characterized by the presence of a pear-shaped genital chamber, protruding behind the posterior part of the accessory gland, with a long duct (Figures 6A and 6B). Black pigmented oviduct in the "loop", after separation of the gono-pericardial duct, is moderately widened (as in *Hydrobia*) and proportionally very long, making several whorls; after that the oviduct continues in an almost straight, not pigmented terminal part of the same width, receiving at the beginning, before the duct of the genital chamber, a rather long duct of the seminal receptacle, and terminating with a genital pore.

Male accessory gland of moderate size; a characteristic flattened penis is present, without any conspicuous outgrowths, with an enlarged, "bubble-like" and turned to the left end (Figure 6C).

Type species: ***Obrovia salaria*** Radoman, spec. nov.

Etymology: This genus is named for the town Obrovac on the Zrmanja river.

By the form of the shell as well as by its anatomy, this genus undoubtedly is related to the genus *Hydrobia*, yet anatomically clearly different from it by the following features: in *Hydrobia* the genital chamber is large, more extensive, the oviduct in the "loop" much shorter, the penis is longer and pointed, with an outgrowth on the middle of the left side (*cf.* Krull, 1935; Radoman, 1955).

Up to now I have found 2 species of this genus which live sympatrically in the brackish part of the river Zrmanja near the town of Obrovac.

Obrovia salaria Radoman, spec. nov.

Shell (Figure 2A) regularly conical, with slightly more tumid whorls and deeper suture than in the next species. Sexual dimorphism of the shells: the females are larger than the males.

Measurements: in Table 2

Table 2

		shell		aperture		number
		length	width	length	width	of whorls
Obrovia salaria	females	3.8 - 4.7	1.8 - 2.1	1.3 - 1.5	1.1 - 1.3	6½ - 7½
	males	3.3 - 3.6	1.3 - 1.6	1.0 - 1.2	0.8 - 1.0	5½ - 6½
Obrovia testadura		3.3 - 4.2	1.6 - 2.0	1.2 - 1.4	0.9 - 1.1	6 - 6½

Explanation of Figure *1*

Figure *1*: (A) ***Semisalsa dalmatica*** Radoman, spec. nov.; (B) ***Semisalsa rausiana*** Radoman, spec. nov.; (C) ***Semisalsa graeca*** Radoman, spec. nov.

Explanation of Figure *2*

Figure *2*: (A) ***Obrovia salaria*** Radoman, spec. nov.; (B) ***Obrovia testadura*** Radoman, spec. nov.


A
B
C

A

B

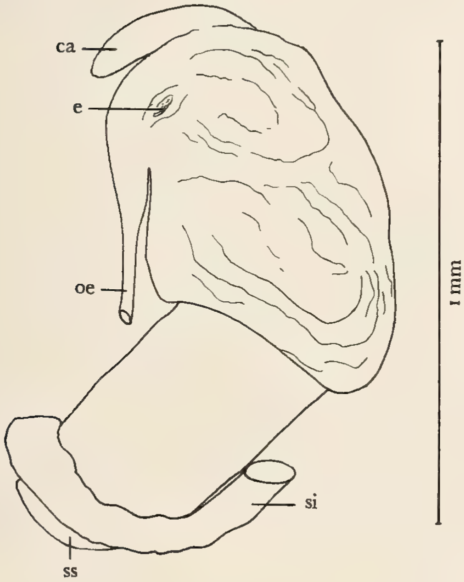

Figure 5

Obrovia salaria Radoman, spec. nov.
ca – caecal appendix other abbreviations as in Figure 3
Radula (above) Stomach (below)

Type locality: the brackish part of the Zrmanja river, near the town of Obrovac in Yugoslavia.

Etymology: the name of the species is derived from the Latin "salarius", meaning "saline".

Holotype: Prirodnjački Muzej, Beograd (PMB) 8000/1; collected in July 1973 by Pavle Radoman

Paratypes: PMB 8000/2 (3); same data as for the holotype

Obrovia testadura Radoman, spec. nov.

Shell (Figure 2B) thick, very hard, smaller than in the females of the type species; although conical, the shell of this species is slightly ovoid in outline by which it is distinguished from the type species.

Measurements: in Table 2

Type Locality: the brackish water of Zrmanja river near the town of Obrovac, Yugoslavia.

Etymology: the species name is derived from the Latin "testa", meaning "shell", and "dura", meaning "hard".

Holotype: Prirodnjački Muzej, Beograd (PMB) 8001/1; collected in July 1972 by Pavle Radoman

Paratypes: PMB 8001/2 (2); same data as for the holotype

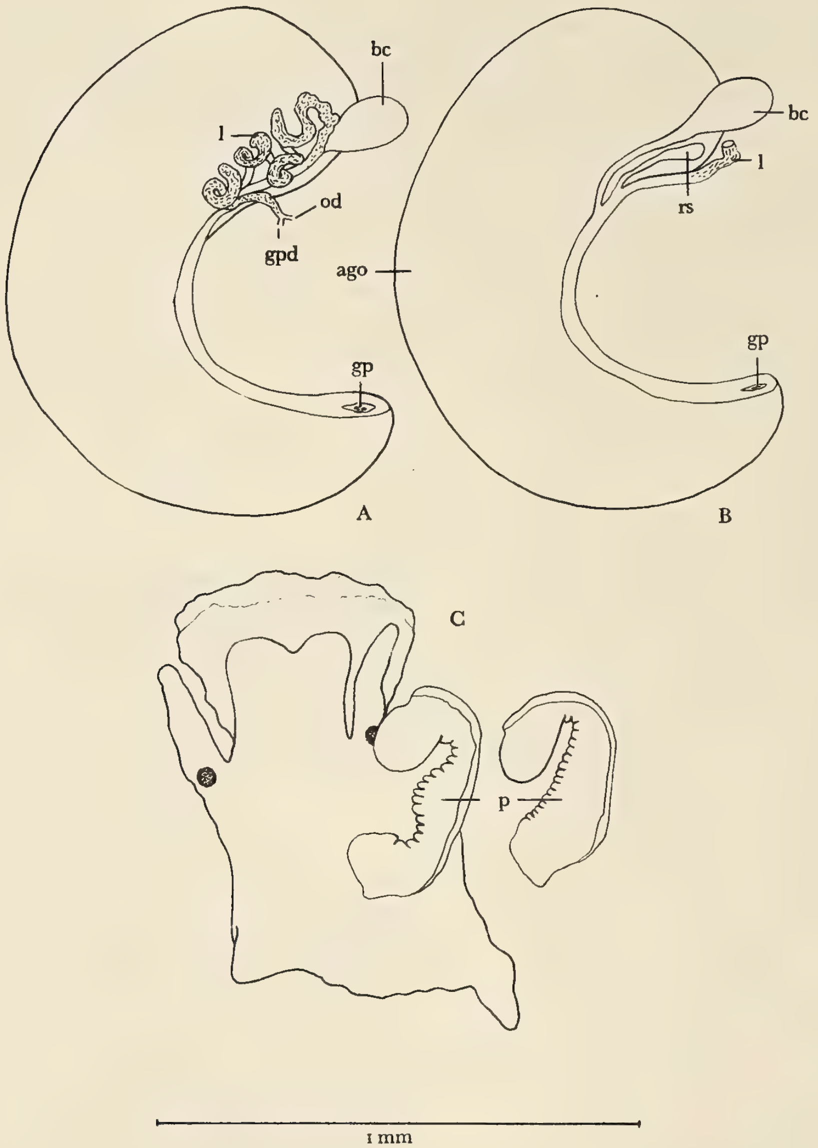

Figure 6

Obrovia salaria Radoman, spec. nov.
A: Female reproductive system (without ovary) in natural position
B: the same, dissected C: Anterior part of male, with penis
gpd – gono-pericardial duct other abbreviations as in Figure 4

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Observations on the Effect of Various Drugs on the Activity of the Preoral Cilia of the Prosobranch Veliger, *Conus californicus* Hinds

BY

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VELIGERS OF *Conus californicus* Hinds, 1844 were obtained from egg capsules that hatched in the laboratory. The veligers were transferred to a 250 ml capacity beaker of filtered (0.45 μm) sea water with a capillary pipette. The water was changed every 3 days and a few drops of a cell suspension of *Phaeodactylum tricornutum* were introduced as food.

Acetylcholine chloride, Flexadil (a curare-like substance) and 5-HT creatine sulfate (serotonin) were tested for their effect on the preoral cilia. Dilutions of the individual drugs were prepared and in each experiment the solution was added to a petri dish, 60 mm in diameter, containing sea water and 10 veligers. The veligers were transferred to a depression slide by pipette and observed under a compound microscope at 35 × and 100 × magnification for preoral ciliary activity. Concurrently, veligers were pipetted out into a depression slide without the drug to serve as control. The pH of the solution was determined with pH paper and was in the range 7.0 to 7.5.

Table 1 lists the results of the effects of various drugs on ciliary activity.

Table 1

Drug	conc. g/ml	Response of preoral cilia
Acetylcholine	10^{-3}	—
	19^{-5}	+
Flexadil	10^{-3}	—
5-HT	10^{-3}	+
	10^{-5}	+

+ = increased activity; — = decreased activity

CARTER (1926, 1928) found that in nudibranchs the cilia do not beat continuously and are under control of nerves in the velum. It is possible that the activity of the preoral cilia is controlled by a chemical transmitter similar to that which has been suggested for cilia of *Mytilus edulis* gills (BÜLBRING, BURN & SHELLY, 1953). These investigators found that acetylcholine at low concentrations, 10^{-5} g/ml and 10^{-6} g/ml, increased ciliary activity and that at high concentrations, 10^{-3} g/ml, decreased activity. LAGERSPETZ, LANSIMIES, IMPIVAARA & SENIUS (1970) found similar effects for high and low concentrations of acetylcholine on gill filament cilia of *Anodonta cygnea*. The results show that the activity of the preoral cilia of *Conus californicus* was inhibited with acetylcholine at 10^{-3} g/ml and stimulated at 10^{-5} g/ml. BÜLBRING, BURN & SHELLY (1953) also found that d-tubocurarine reduced ciliary activity. A curare-like substance, Flexadil, was tested on the veligers and it did depress the activity of the preoral cilia.

The veligers were observed feeding when acetylcholine was used. However, when serotonin was added, feeding was not evident. The cilia were beating rapidly and rejection currents may have been set up which prevented the algal cells from reaching the food groove (FRETTER & MONTGOMERY, 1968).

Further studies need to be performed to determine what chemical transmitter controls the preoral cilia.

ACKNOWLEDGMENT

I wish to thank Dr. Vera Fretter of the University of Reading, England, for her criticism and guidance throughout the experiment.

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Sabia conica (Schumacher) on the Pacific Coast of North America

BY

I. McTAGGART COWAN

(1 Plate)

Three specimens of *Sabia conica* (Schumacher, 1817) from the Queen Charlotte Islands were taken by Dr. Frank Bernard of the Canada Department of Environment, Biological Station, Nanaimo, British Columbia, on August 17, 1963, at Tasu Harbor, Q. C. I., British Columbia.

The 3 specimens were attached to a living abalone (*Haliotis kamtschatkana* Jonas, 1845). No others have been found in the examinations of many hundreds of live-taken specimens of *Haliotis* and other mollusks from the coast of British Columbia.

Two of the *Sabia* specimens retain the larval shell; one of these preserves the surface detail (Figures *1* and *2*). Comparisons of these specimens with the large series representing other species in the Atlantic and Pacific faunas reveal some unique features. However, the resemblance to *Sabia conica* of the Indo-Pacific region is so close that, until additional living specimens are secured, I do not feel justified in naming a new species.

Griffith (1967) reported *Hipponix tumens* from Table Island, Queen Charlotte Sound, British Columbia, on the basis of a single specimen taken alive attached to a stone in the intertidal zone. She has permitted me to examine the specimen. It is clearly not *H. tumens* (Figure *3*) but seems to me to be an adult shell of *S. conica* (Cowan, 1974). It differs from specimens of this species from the tropical Pacific in whitish rather than brown colour, slightly larger and more clearly defined muscle scars and in some minor details of sculpture. Details of form, sculpturing and colour of the specimens from Tasu Harbour are within the range of variation of *S. conica*.

Thus *Sabia conica* is now reported from two localities, separated by more than 160 km, on the British Columbia coast of the N. E. Pacific Ocean. The areas of occurrence are close to that in which Clarke (1972) has recorded another Indo-Pacific gastropod, *Clanculus microdon ater* Pilsbry, 1911.

The northward distribution of *Sabia conica* elsewhere in the Pacific extends to Hawaii (Tinker, 1958) and to about the 43rd parallel (southern Hokkaido) along the coast of Japan (Kuroda *et al.*, 1971).

The British Columbia localities are in year round cold water (mean annual absolute maximum and minimum $12\frac{2}{3}$° C and 6 5/9° C) and beyond the normally understood tolerance of the species. Tasu Harbour, Q. C. I., is the location of a metal mine that has exported much of its product to Japan on Japanese vessels. These could have introduced larvae to the locality. The Table Island site could have received an introduction from passing ships – many Japanese vessels ply the adjacent strait.

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Explanation of Figures *1* to *3*

Figure *1*: *Sabia conica* from Queen Charlotte Islands, British Columbia, external features of shell 4.8 mm

Figure *2*: *Sabia conica* larval shell showing longitudinal sculpture below

Figure *3*: *Sabia conica* Table Island, British Columbia (mature specimen)

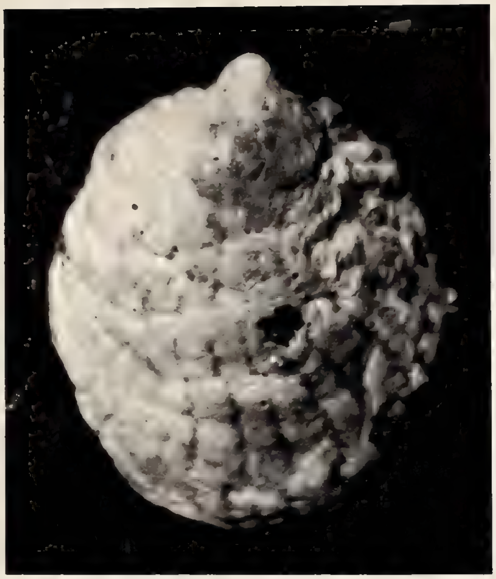

Figure *1*

Figure *2*

Figure *3*

Notes on Mating Behaviour of *Concholepas concholepas*

(Mollusca : Gastropoda : Muricidae)

from Chile

BY

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Concholepas concholepas (Bruguière, 1789), a muricid snail commonly known in Chile as "loco", is commercially the second most important mollusk in this country. Hancock (1969) estimated that the 4000 tons of this snail landed in Chilean ports in 1967 had a value of US $ 1 140 000. The species is found only on the Pacific coast of Chile and Perú (Dall, 1909; Carcelles, 1954).

Little is known about the sexual behaviour of *Concholepas concholepas*. During the austral summer of 1973 I started investigations on this species and made some observations on its mating behaviour.

Concholepas concholepas is a dioecious species lacking externally evident sexual dimorphism. Huaquín (1966) described the external and internal anatomy of this mollusk. Guzmán *et al.* (1972) carried out a histological study of the male reproductive system. The male has a conspicuous penis situated at the base of the right tentacle, close to the eye, and is large enough to be seen by the naked eye. Nevertheless, it remains normally hidden beneath the shell. Therefore, in order to carry out observations on mating behaviour I previously developed a technique for sexing the living animal. This technique was adapted from that described by Wong & Wagner (1954) and by Hargis (1957) for gastropods. Animals were carefully detached from the aquarium by sliding them from the vertical walls or, alternatively, by inserting a knife under the foot. They were placed upside down, individually, in the middle of a glass or plastic tray with running sea water for about 3 to 5 minutes. When the foot began to move, the animal was turned slightly, at about 45° to the vertical, so that its right side faced upwards, the anterior end of the shell nearly touching the wall of the tray. The positioning of the animal must be done in quiet water using only the amount necessary to cover half of the specimen. Care must be taken that the inhalant siphon, situated on the left side of the animal, remains covered at all times. After 1 to 4 minutes most of the animals in this position begin to extend the anterior part of the foot and attach it to the wall of the dish. When the anterior part of the foot is well attached to the wall it is possible, by careful traction on the anterior part of the shell, to see the base of the right tentacle where the penis is easily seen if the specimen is a male. Direct lighting of the area under observation should be delayed until the last moment of the traction action, when the tentacle area is clear. Using this technique we have successfully sexed specimens of *Concholepas concholepas* of from 2.0 to 14.0 cm maximum shell diameter.

Mating behaviour and copulation were observed in a group of 10 "locos" collected on the 20th of February 1973 from the intertidal area of Isla Ritoque (71°32′S; 33°53′ 20″W) off the mouth of the river Aconcagua, Valparaíso. The animals were brought to the laboratory, sexed, and the shell marked with paint before placing them in a glass tank of 8 l capacity with circulating sea water and aeration. Observations were carried out during day and night from the 22nd to the 27th February. No food was offered to the animals during this period. The temperature of the water during the observations ranged from 16.5° to 18° C. No illumination was provided at night, observations being made in the dim light of a hand torch.

The first couple of "locos" copulating was observed on February 22nd at 00.30; another couple at 01.00. On the 23rd copulation was observed at 23.00 (the male of the first copulation observed participated again). On the 26th, copulation of a new pair was observed at 21.00. No mating behaviour was observed at any time during daylight during the whole week of observations. The locomotor

activity of *Concholepas* increased markedly towards 20.00 to 21.00 every night and decreased towards 06.00 to 07.00 in the morning.

Copulation was observed to occur in one of two ways: 1. – male mounting the female (mounting position), or 2. – both male and female remaining on the substratum (non-mounting position). In both cases the male guided the penis towards the right side of the mantle aperture, where the female genital pore is situated. In the mounting position the pair was observed to form a cross, with the anterior end of the male over the right side of the female. In the non-mounting position two situations were observed:

a. – male and female facing one another;

b. – male facing the posterior end of the female.

In the latter case the penis was introduced into the posterior end of the right pallial groove of the female and slid forward until it reached the genital pore. When the pair maintained this position it was possible to measure the maximum extension of the penis. In one case observed, a male of 8.5 cm maximum shell diameter and a female of 9.0 cm shell diameter, the extension of the penis was about 5.5 to 6.0 cm.

All copulations observed lasted between 2 and 5 minutes. The criterion for the beginning of copulation was taken as the active movement of particles in the interior section of the penis visible to the observer during the act; the criterion for its termination was the extraction of the penis from the pallial cavity.

ACKNOWLEDGMENTS

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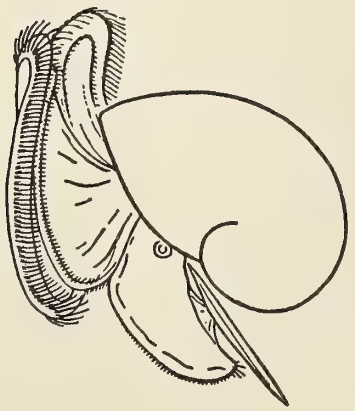

Styliola sinecosta, a New Species of Pteropod

(Opisthobranchia : Thecosomata)

from Barbados, West Indies

BY

FRED E. WELLS, Jr.

Marine Sciences Centre, McGill University, Montreal, Quebec, Canada

(3 Text figures)

DURING A TWO YEAR zooplankton sampling program at Barbados, West Indies, several individuals of a new species of the thecosomatous pteropod genus *Styliola* were collected (WELLS, 1973). The species was collected at intermittent intervals and had an average abundance of 2.2 individuals per 1000 m^3 of water, compared to 2949.3 for *Spiratella inflata* (d'Orbigny, 1836), the most abundant thecosome, and 18.5 for *Styliola subula* (Quoy & Gaimard, 1827).

OPISTHOBRANCHIA

THECOSOMATA

Euthecosomata

CAVOLINIIDAE

Styliola Gray, 1850

Styliola sinecosta Wells, spec. nov.

Holotype: An immature individual collected in the upper 300 m of water at a station 5 km west of the Bellairs Research Institute, St. James, Barbados (13°11′N; 59°41′W) on 27 July 1972. Deposited at the National Museum of Natural Science, Ottawa, Ontario, Canada, specimen no. 69251.

Paratypes: Three smaller individuals collected with the holotype and 8 individuals collected at the same station on other dates. Specimen numbers of the paratypes are given in Table 1.

Diagnosis: Shell conical, slightly curved, aperture circular. There is no sculpture on the shell, but faint growth lines can be seen. The posterior embryonic shell is rounded at the posterior tip. The posterior foot lobe is tongue-shaped (Figure 1, PFL); the relatively small wings are narrow and lack tentacles on the anterior border. A mantle extension, on the left side, the excurrent siphon (formerly known as the 'balancer') is present, and the body is yellowish in freshly preserved material.

Measurements: Details of the shell measurements of the holotype and paratypes are given in Table 1. The specimens range in total shell length from 0.72 to 4.25 mm and in maximum width at the aperture from 0.22 to 1.08 mm. The length/width ratio varies from 3.21 to 4.13. The embryonic shells are of similar size, ranging from 0.35 to 0.42 mm in length and from 0.12 to 0.18 mm in width.

Remarks: *Styliola sinecosta* has probably been misidentified as *Creseis virgula clava* (Rang, 1828) by CHEN & BÉ (1964). *Creseis virgula clava* was originally described as *Cleodora clava* by Rang, who pointed out the close similarity with *Creseis acicula* (Rang, 1828). Both *Creseis virgula clava* and *C. acicula* have a length/width ratio of over 10 to 1, in contrast to the figure by Chen and Bé, which shows a ratio of about 4 : 1. Although no anatomical data were given by Chen and Bé it appears likely that they were dealing with *Styliola sinecosta*, not *C. virgula clava*. *Creseis virgula clava* is a long, thin form more closely related to *C. acicula* than to *C. virgula*, prompting SPOEL (1967) to suggest that it should be considered a subspecies of *C. acicula*, *C. acicula clava*.

Creseis virgula, the type species of the genus *Creseis*, has tentacular lobes on the anterior wing margins (Figure 2, WT), has a short posterior foot lobe (PFL), well developed, broad wings and a white body color in preserved specimens. *Styliola sinecosta* differs in all 4 characterist-

ics, and thus cannot be a *Creseis.* The only other genus with a conical shell is *Styliola,* which has no wing tentacles, has a tongue-shaped posterior foot lobe, narrow wings and yellow body color In all 4 characteristics *Styliola*

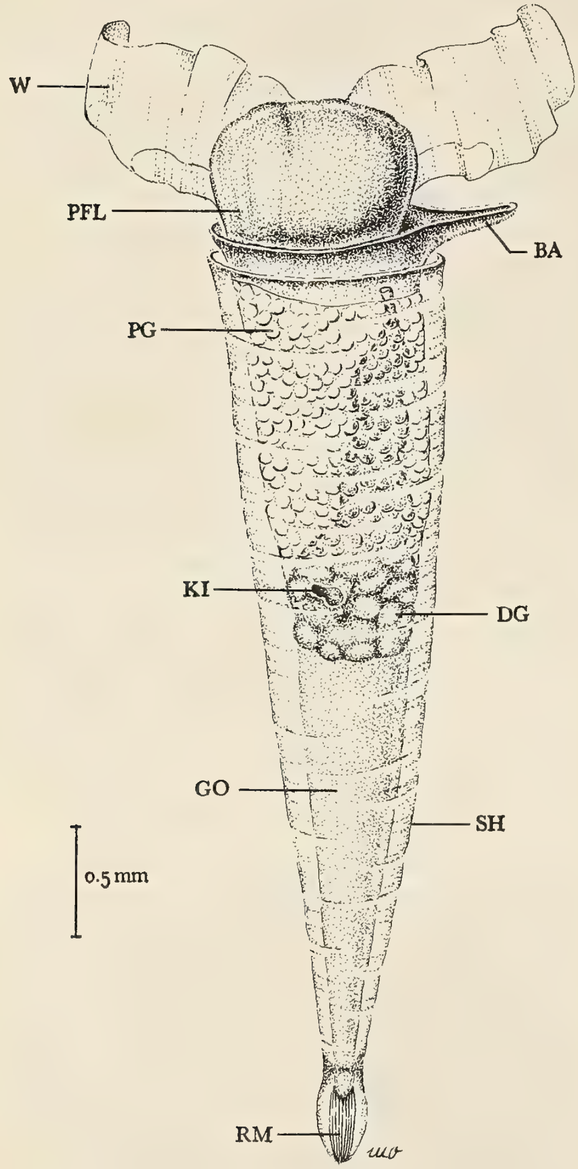

Figure 1

Ventral view of *Styliola sinecosta* Wells, spec. nov.

BA – excurrent siphon ("balancer") DG – digestive gland GO – gonad KI – kidney PFL – posterior foot lobe PG – pallial gland RM – retractor muscle SH – shell W – wing

sinecosta matches the characteristics of the genus *Styliola.* The shell of *S. subula,* the only other species of the genus, is similar to that of *S. sinecosta,* but *S. subula* has a pronounced dorsal ridge which develops after the animal has attained 1.1 mm in total shell length (Figure 3). The largest specimens of *S. sinecosta,* 3.00 and 4.25 mm long, clearly lack a shell rib, prompting the species name *sinecosta,* which means 'without rib'. Smaller individuals of *S. subula* can be differentiated from *S. sinecosta* by differences in the embryonic shell (Figure 3), which is slightly swollen and rounded posteriorly in *S. sinecosta* and is pointed at the posterior tip in *S. subula.*

Geographical Distribution: All specimens described here were collected off Barbados. Chen & Bé (1964) recorded specimens from their Station Delta, 700 km southeast of Greenland (44°00′N; 41°00′W); from Station Echo, in the north central Sargasso Sea (35°00′N; 48°00′W); and from Bermuda. *Styliola sinecosta* has not yet been reported between Barbados and Bermuda, but it is likely that a search of plankton samples in intermediate areas would show that the species occurs there also.

ACKNOWLEDGMENTS

I thank Dr. Arthur H. Clarke of the National Museum of Natural Science and Dr. C. M. Lalli of the Marine Sciences Centre for many helpful suggestions. Mrs. D. C. Maclellan suggested the species name. M. Oeltzchner did the final preparation of the figures. Supported by Grant A 5248 from the National Research Council of Canada to Dr. C. M. Lalli.

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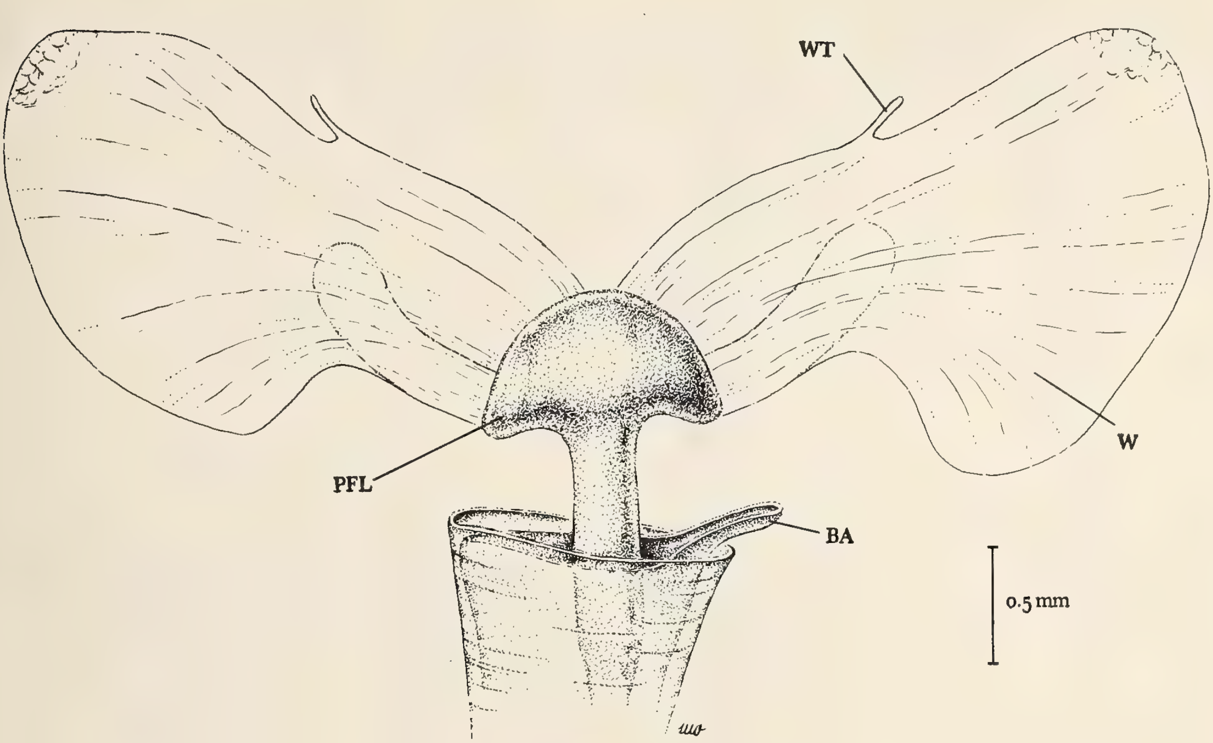

Figure 2

Ventral view of the wing area of *Creseis virgula*

BA – excurrent siphon ("balancer") PFL – posterior foot lobe
W – wing WT – wing tentacles

Table 1

Measurements of the holotype and paratypes of *Styliola sinecosta* Wells, spec. nov.

Date collected	type	specimen number	Total shell measurements Length (mm)	Width (mm)	Length/Width Ratio	Embryonic shell measurements Length (mm)	Width (mm)
27 July 1972	Holotype	69251	4.25	1.08	3.95	0.38	0.18
	Paratype	69252	3.00	0.72	4.13	0.42	0.18
			1.88	0.55	3.41	0.35	0.18
			1.00	0.30	3.33	0.35	0.18
28 June 1971	Paratype	69256	1.48	0.42	3.48	0.40	0.18
			1.25	0.35	3.57	0.38	0.15
			1.12	0.35	3.21	0.38	0.18
			1.05	0.30	3.50	0.40	0.18
			0.72	0.22	3.22	0.38	0.18
11 November 1972	Paratype	69253	1.30	0.38	3.47	0.35	0.12
3 March 1973	Paratype	69254	2.28	0.68	3.35	0.40	0.18
21 March 1973	Paratype	69255	1.50	0.42	3.53	0.38	0.15

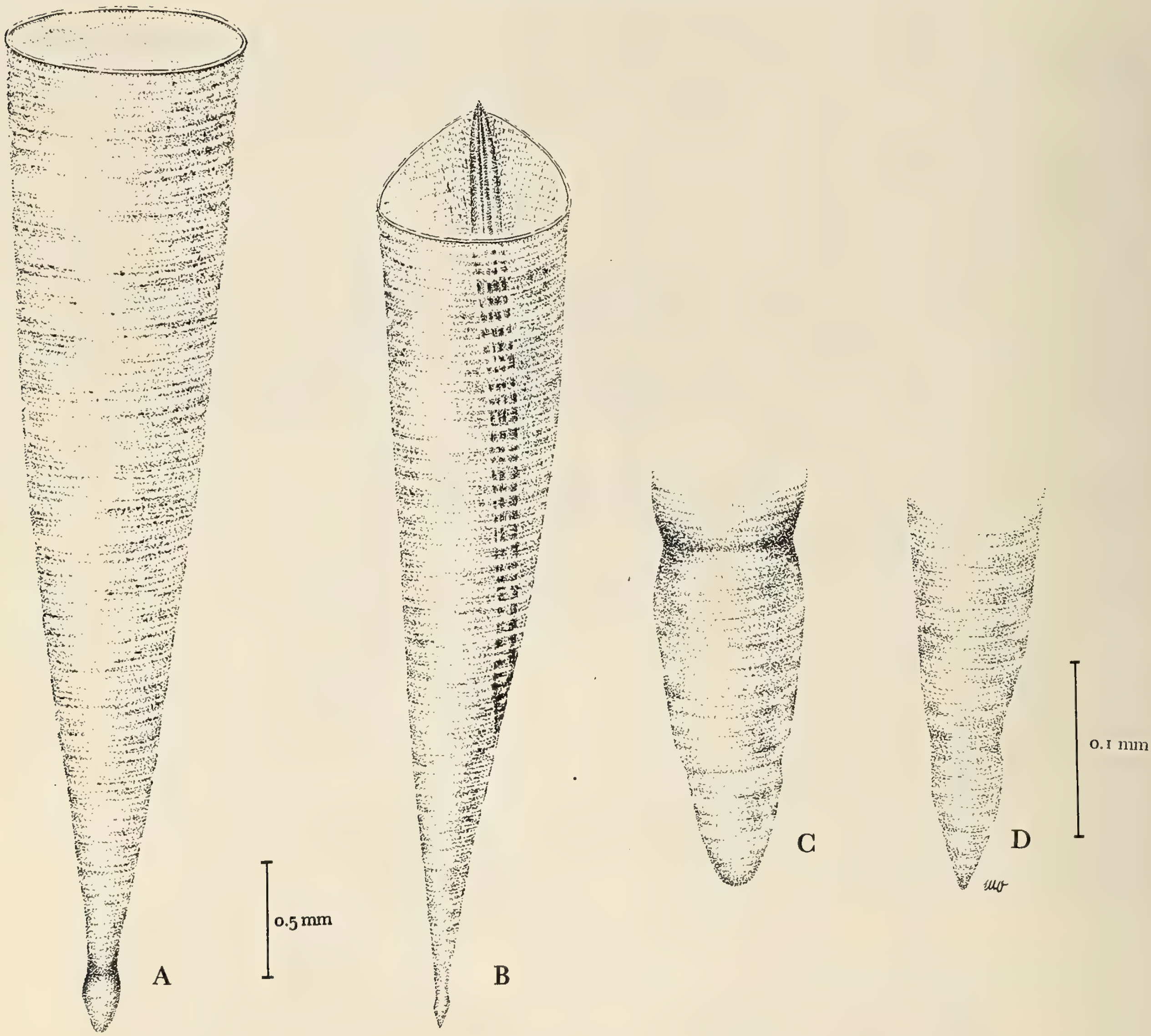

Figure 3

Comparison of shells of *Styliola sinecosta* and *Styliola subula*

A: Complete shell of *Styliola sinecosta.* B: Complete shell of *Styliola subula.* C: Embryonic portion of shell of *Styliola sinecosta.* D: Embryonic portion of shell of *Styliola subula.*

A New Subspecies of *Cyanoplax dentiens* (Polyplacophora) from San Diego, California

BY

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(1 Plate)

INTRODUCTION

Cyanoplax dentiens (Gould, 1846), as presently defined (Berry, 1948), has an extensive eastern Pacific range that extends from Alaska to Magdalena Bay, Baja California (Burghardt & Burghardt, 1969). The species is a common inhabitant of rocky shore intertidal and shallow-water zones north of Point Conception, California, but is rarely found to the south. Recently, extensive skin-diving around San Diego has revealed a population of chitons that appears to be related to *C. dentiens* in some ways, while possessing distinctive characteristics of its own. Because of its obvious differences, both morphological and ecological, from *C. dentiens*, this population is here described as a subspecies, an assignment which should be regarded, for the present, as tentative. *Cyanoplax dentiens* is a rather variable species throughout its great range, and the exact relationships of this San Diego group to it must wait until more information is available concerning the nature of *C. dentiens* in the southern part of its range.

SYSTEMATICS

POLYPLACOPHORA de Blainville, 1816

NEOLORICATA Bergenhayn, 1955

Ischnochitonidae Dall, 1889

Cyanoplax Pilsbry, 1892

Cyanoplax dentiens ***cryptica*** Kues, subspec. nov.

Diagnosis: Small (to 19 mm), broadly elongate in outline with the length-width ratio averaging about 1.7. Valves highly arched for genus, with slightly convex slopes; jugum rounded and beaked. Girdle encroaching between sutures for about $\frac{1}{4}$ to $\frac{1}{3}$ of distance to apex of jugum. Surface of tegmentum smooth to naked eye; covered with minute granulations visible at $20\times$ or higher magnification. Ctenidia 18 - 20 in number, extending almost to head. Color a distinctive red-brown, with small blue-green dots on valves.

Description: Head valve evenly crescentic, with anterior slope convex, randomly and densely covered with small rounded granules, decreasing in size towards apex in younger individuals; granules flatter in older ones, obsolete in some areas; concentric growth lines visible, predominantly near girdle.

Intermediate valves with lateral areas almost imperceptibly raised, sculptured with minute elongated granules, larger near the girdle, giving the impression of being arranged in radial lines. Central areas smoother than lateral areas, composed of very faint, flattened, elongated granules, also seeming to be in longitudinal rows which curve away from the jugum anteriorly. In many specimens most of the central area is worn to virtual smoothness. Underneath surface of tegmentum dark, longitudinal, sometimes anastomosing lines may be seen in wet specimens; these more pronounced when granulations are obsolete. These are the fiber tracts of the aesthete system. Jugal beaks prominent and inflated. Valve divergence approximately 105°; the side slopes are slightly convex. Concentric growth lines present.

Tail valve small, with posterior area sculptured like head valve; central area smoother, much like equivalent part of intermediate valves. Mucro elevated, anterior; posterior slope of valve flat to slightly convex.

Interior of valves with articulamentum translucent blue, becoming white beneath jugum and towards

front of valves. Sutural laminae prominent, thin, and flaring; sinus fairly wide. In the middle, beneath the jugum are many transverse slits, sometimes broadening at places into elongate holes, becoming spongy near sinus. Slit rays deep, possessing a line of small round pores in the intermediate valves. The eaves, virtually non-existent, are porous and the teeth extend far beyond the limits of the tegmentum. Slit formula is 8-9, 1-1, 9-10. The slits are deep and the teeth square.

Girdle wide and smooth, with the rather gritty appearance characteristic of the genus, and extending between the intermediate valves usually about $\frac{1}{3}$ of the distance to the jugum.

Color of the dorsal valve surfaces a dark, rich, red-brown, brightest at the jugum, with the girdle somewhat lighter and unbanded; this is exactly the color of the brown alga *Eisenia arborea* on which the chiton lives. Occasionally the jugal areas have a splotch of white, and on every valve there are always small, round, blue-green dots, sometimes limited only to the lateral areas of the intermediate valves.

Measurements (of holotype): maximum length 15.2 mm; shell length 13.5 mm; maximum width 9.2 mm; shell width 6.5 mm; height 3.0 mm. Approximately 12 specimens have been collected; the largest measures 19×10 mm and the smallest 3.0×1.7 mm.

Disposition of Material: The holotype, a whole specimen preserved in alcohol, is number 51310 in the San Diego Museum of Natural History invertebrate collection; a paratype has been deposited in the United States National Museum of Natural History as USNM 735015; the disarticulated valves, from a second paratype, have been deposited in the Geology Type collection of the California Academy of Sciences, where they have been given the number 53589.

Type Locality: The holotype and paratypes are from Bird Rock, La Jolla, California (32°48′54″N; 117°16′30″W); on *Eisenia arborea* in surge channels in a depth of about $\frac{1}{2}$ m at very low (-1.5) tide. Other specimens have come from *Eisenia* holdfasts in 3 to 6 m of water off Devil's Slide, La Jolla, and from False Point, La Jolla, also on holdfasts.

DISCUSSION

This subspecies is unusual because it appears to be restricted to the common southern California kelp *Eisenia arborea*. This is the first report of any chiton living on this kelp. The color of the chiton is almost exactly the same as that of the kelp, suggesting that it spends all or most of its existence there. Gut content analysis of several specimens has shown that the kelp is the only source of food. Some specimens were found situated in shallow depressions in the kelp which they had apparently eaten away in the fashion of *Acmaea insessa* (Hinds, 1842) on the stipes of the kelp *Egregia*. ***Cyanoplax dentiens cryptica*** has been found in 3 places on *Eisenia*: on the stipes, just above where the stipe bifurcates (usually in among small fronds); on the holdfasts; and on the upper surface of the fronds. The specimens from the holdfasts were on the average about one half as large as those from the stipe and fronds, and specimens only came from larger plants which were always subtidal. Moreover, the chitons were found on only a small percentage of the total plants examined, but when they were present, there was usually more than one individual on a plant. These observations suggest that the young animals either orient to larger plants before settling, or are unable to survive for long on smaller plants. The stability of the kelp may be an important factor, since the smallest representatives have all come from the most stable part of the plants – the hold-

Explanation of Figures *1* to *9*

Figure *1*: Dorsal view of holotype, SDMNH 51310 × 6
Figure *2*: Side view of paratype, USNM 735015 × 6
Figure *3*: Dorsal view of head valve, paratype, Calif. Acad. Sci. × 8
Figure *4*: Dorsal view of intermediate valve 3, paratype, Calif. Acad. Sci. × 8
Figure *5*: Dorsal view of tail valve, paratype, Calif. Acad. Sci. × 8
Figure *6*: Ventral view of head valve, paratype, Calif. Acad. Sci. × 8
Figure *7*: Ventral view of intermediate valve 3, paratype, Calif. Acad. Sci. × 8
Figure *8*: Ventral view of tail valve, paratype, Calif. Acad. Sci. × 8
Figure *9*: Anterior view of intermediate valve 3, paratype, Calif. Acad. Sci. × 10

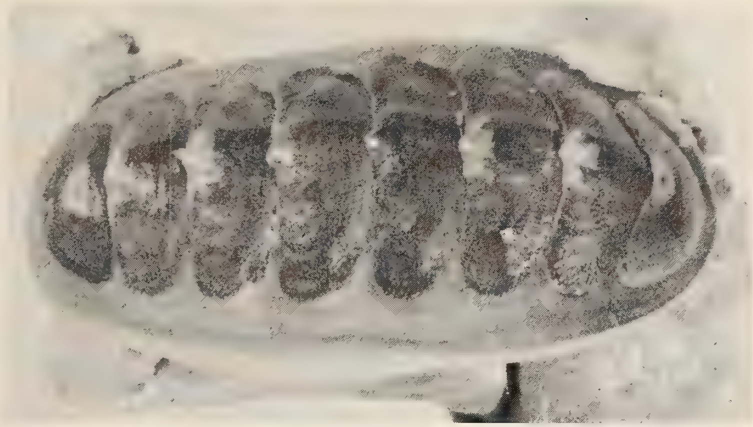

Figure *1*

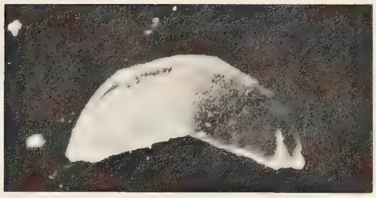

Figure *3*

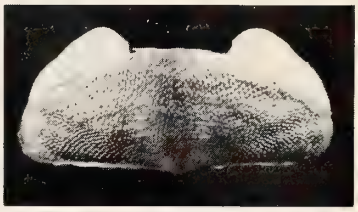

Figure *4*

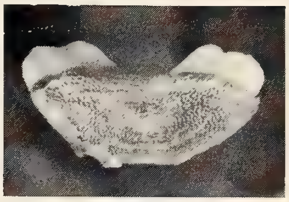

Figure *5*

Figure *2*

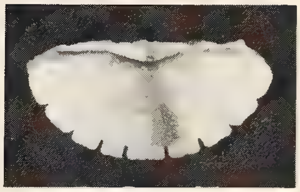

Figure *6*

Figure *7*

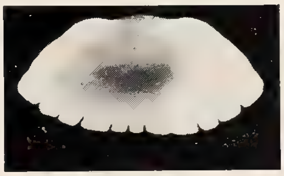

Figure *8*

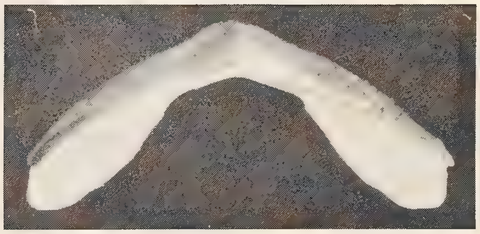

Figure *9*

fasts. Perhaps the smaller kelp plants are buffeted about too severely by currents to allow establishment of the chitons on them.

In the course of dissecting some specimens collected in March, 1969, it was observed that the gonads were large and the eggs well developed, indicating that this subspecies spawns in the spring. Whether spawning occurs at other times is unknown, though specimens collected in August and September had small gonads.

REMARKS

Cyanoplax dentiens cryptica cannot be mistaken for any other southern California *Cyanoplax*. It is easily distinguished from *C. hartwegii* (Carpenter, 1855) by its smaller size, color, and the greater girdle encroachment between the valves. From *C. lowei* (Pilsbry 1918) it is distinguished by the lack of any radial impressions on the anterior and posterior valves, the anterior position of the mucro and the small eaves. From previously described examples of *C. dentiens*, this subspecies differs morphologically in several features: (1) the coloration is consistently red-brown with blue-green dots instead of various shades of blue, slate and brown; (2) the girdle is wider and extends to a greater degree between the valves; (3) the slopes of the valves are generally convex rather than tending to concavity; (4) the valves are more highly arched; (5) the lateral ends of the intermediate valves are rounded instead of having a squarish aspect; and (6) it has smaller, less obvious granulations in the central areas of the valves. Of equal or greater import are the ecological differences between *C. dentiens* ***cryptica*** and *C. d. dentiens*. The former is restricted to a very narrow habitat, namely the kelp *Eisenia arborea*, while the latter is an intertidal and shallow-water rock dweller which has never been reported from this kelp. The association of a molluscan species with a specific alga is unusual but by no means unknown. Test (1945) reported that the limpet *Acmaea insessa* is restricted to the kelp *Egregia menziesii* (Turner) Areschoug, and *A. instabilis* (Gould, 1846) to the stipe of *Laminaria andersonii* Eaton. The chiton *C. lowei* is similarly restricted to *Macrocystis* holdfasts, and *C. fackenthallae* Berry, 1919 lives in the holdfasts of the ribbon kelp around Monterey (Smith & Gordon, 1948). In all cases, these organisms take on the color of their algal substrate, as *C. d.* ***cryptica*** has done. If *C. d.* ***cryptica*** is, in fact, entirely limited to *Eisenia arborea*, as it appears to be, genetic interchange with populations of *C. d. dentiens* (which are rare in this area, anyway) would be slight or lacking, and *C. d.* ***cryptica***, though morphologically not highly differentiated, could be considered a separate species, as that term is defined by Mayr (1970: 12-13). In view of the fact that more information is needed concerning both *C. d. dentiens* and *C. d.* ***cryptica***, it seems prudent at this time to leave the latter as a subspecies.

At present, *Cyanoplax dentiens* ***cryptica*** is known only from San Diego, but the range of *Eisenia arborea* may provide a clue to its real distribution. Hollenberg & Abbott (1966) report that this kelp is common from Magdalena Bay, Baja California to Redondo Beach, California and appears sporadically north to Monterey and even to Vancouver Island, Canada. It is likely that *C. d.* ***cryptica***, like many other chiton species, will be found to be limited to southern California and the Pacific coast of Baja California.

Cyanoplax dentiens ***cryptica*** is not very common, and it is probably due to this fact and its restricted habitat that it has thus far been overlooked. This subspecies may include the unidentified form mentioned by Pilsbry (1918: 127). His specimen was "red with blue-green spots, from San Pedro." He was uncertain of its identity because it hadn't been disarticulated, and nc more was ever said about it.

The subspecific name comes from the Latin *crypticus* which means "hidden" and refers to the habitat of the chiton, concealed beneath the holdfasts or under the fronds of the kelp.

ACKNOWLEDGMENTS

This work is part of a master's thesis dealing with several aspects of southern California chitons submitted to Scripps Institution of Oceanography. I wish to thank Dr. William A. Newman, of that Institution, for his invaluable guidance during the course of the study and in the preparation of the original manuscript. My thanks go also to Dr. Alan S. Horowitz, Department of Geology, Indiana University, for critically reading a revised version of the manuscript.

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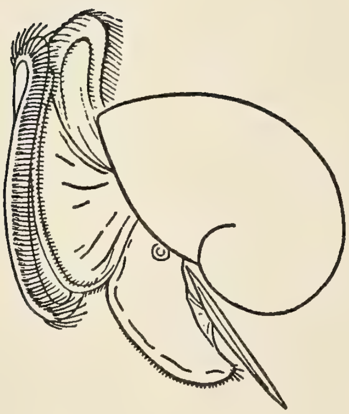

Estimates of Growth of *Cryptochiton stelleri* (Middendorff, 1846) in Oregon

BY

JOHN BEACH PALMER [1] AND PETER WOLFGANG FRANK [2]

DURING 1964 AND 1965 PALMER (1968), in connection with a study on the interrelation between the polynoid worm *Arctonoe vittata* (Grube, 1855) and its hosts, marked and measured the size of a number of *Cryptochiton stelleri* (Middendorff, 1846). The marking method proved feasible. Although tags were lost at a considerable rate, they seemed not to be injurious in any major way; some remained for periods of a year or more. Moreover, the initial data of Palmer, although difficult to interpret because precise measurements on living animals are well-nigh impossible, suggested that additional work would prove worth-while. Thus Frank instituted a marking program in June 1968, from which further recaptures are available. Joseph Standaert, an undergraduate research participant sponsored by N. S. F., helped with the marking. During subsequent summers, David Policansky and Carolyn Cross searched for marked animals. This analysis of growth was partly supported by N. S. F. Grant GB 5032 to Frank.

ANIMALS AND THEIR TREATMENT

In different parts of the study, *Cryptochiton* were marked and replaced in several areas within 8 km south of the mouth of Coos Bay, Oregon. The majority of the recaptures are from Cape Arago. Most animals were recaptured within 20 m of the point of release (where this was known precisely enough), even after 2 years. Although Palmer sampled populations by diving, in water to 10 m depth, the other data are almost entirely from the intertidal zone and to ½ m below spring low tides.

Marking was with a loop of 8 - 10 lb. test monofilament nylon to which colored glass beads were attached for identification. The loop was sewn through one side of the girdle so that it penetrated the animal for a distance of about 3 cm. A complete loop was formed by knots coated with methacrylate plastic. Marking was done both in the field and at the Oregon Institute of Marine Biology in nearby Charleston.

Because of considerable changes in dimensions when the animals bend, and the difficulty in getting them to attain a standard relaxed condition after handling, length measurements are virtually useless. Measurements of circumference with a tape are somewhat better but still yield highly variable results. Weight is the only feasible means of estimating size. However, weight is affected by the precision of the balance, the water adhering to the surface of the animal, the amount of food in the gut, and the variable amount of gonadal material as well as by somatic tissues and shell. Palmer tried weighing animals in water and in air, and finally settled on air weights as more repeatable than other measures. A minimum estimate of the amount of variation introduced by imprecision of the balance combined with change in gut contents is available from pairs of weights obtained at succeeding recaptures not more than 4 days apart for 32 animals. The standard deviation of the difference in pairs of weights was 32.6 g. So high a value is, of course, not conducive to precision of the growth analysis. It is, however, an inescapable element in it.

We have useful data from 228 animals recaptured a total of 398 times. There was an interval of at least 3 months between initial marking and release, and first recapture; and between all subsequent recaptures. No estimates of mortality are possible because tag losses were high and variable. In one area where more than 300 animals were released in the summer of 1968, it was apparent by fall that tags were disappearing at an unusually high rate. In this area sea urchins (*Strongylocentrotus* spp). were abundant. It is an index to their activities that on every visit during the fall monofilament tags chewed by them could be found on about 20% of the marked chitons. By spring of the next year virtually all tags had disappeared.

We have one-year records for 71 chitons, two-year records for 9 chitons, and 3-year records for 3 chitons. A year, for our purposes, is from 350 to 380 days.

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Besides recapturing marked animals, we made general observations on movements and feeding rates. Spawning among a group of individuals was observed once in the field. Individuals were dissected once a month for checks on feeding and reproduction. An insufficient number of animals were sacrificed, however, to yield statistical information comparable to that of TUCKER & GIESE (1962) on spawning cycles 6°50′ lat. farther south.

RESULTS

The MACGINITIES (1968) and TUCKER & GIESE (1962) have remarked on the rarity of small animals in the field. Although a special search for young chitons was made and more than 20 (weighing 50 g or less) were marked, we were unable to find any of these small chitons at the end of a year. Table 1 indicates the pattern of growth as observed. The data from recaptures for periods shorter than a year, among them some recaptures of small animals, are dealt with below. From the data, the normal pattern of animal growth, with a maximal increment for intermediate weights, seems to hold. Most individuals encountered in the field range from 20 - 30 cm in length when relaxed and weigh between 500 and 800 g. Although the MacGinities estimate age (from growth lines on the shell plates) of such an average animal at roughly 12 years, this estimate looks on the high side on the basis of our data, which are for a different area. Incidentally, we were unable to find clear indications of growth lines numbering more than 7 in shell plates of animals of any size. From the growth data, best estimates for ages of animals weighing 400 g is probably 5 years; for 800 g, 8 years; and for 1 200 g, 16 years. However, this is interpreting the data rather more precisely than they deserve. Certainly *Cryptochiton* is relatively long-lived, at least off the Oregon coast, with a maximum longevity of more than 20 years. Some further indications validating the growth data in Table 1 and extending them come from the few 2- and 3-year records we have, and from shorter period recaptures of small individuals. It is probably best to recount the 2- and 3-year growth records individually.

Table 1

Growth as measured by annual change in weight of *Cryptochiton stelleri* of various sizes

Weight range (g)	Avg. change in weight per year	S D	N	S E
300 - 399	93	--	1	--
400 - 499	90.8	81.6	10	25.8
500 - 599	136.2	99.6	17	24.2
600 - 699	114.9	76.7	12	22.2
700 - 799	155.0	99.0	9	33.0
800 - 899	49.8	58.1	16	14.5
900 - 999	58.1	70.0	8	24.7
1 000 - 1 099	46.6	75.8	5	33.8
1 100 - 1 199	--	--	-	--
1 200 - 1 299	59	5.7	2	4.0

Animal No. 577 weighed 450 g on August 8, 1968. It weighed 530 g on June 1, and 525 g on August 13, 1969. It was last found on July 19, 1970, when it still weighed 525 g.

Animal No. 583, with an initial weight of 760 g in August 1968, had lost 60 g by the next January, and had regained its original weight a year after marking; by July 1970, this animal weighed 925 g.

Animal No. 594, with an initial weight of 580 g in August 1968, fluctuated within 30 g of this weight during 3 recaptures; at its 4^{th} recapture in June 1970 it weighed 600 g.

Animal No. 595, with an initial weight of 820 g on August 8, 1968, gained 140 g the first year, but weighed only 950 g almost 2 years later on July 17, 1970.

Animal No. 596, with an initial weight of 885 g in August 1968, weighed 1 010 g the next May, only 950 g in July 1969, and was down to 900 g by that September. By July 1970, its recorded weight was 1 115 g.

Animal No. 598, with an initial weight of 720 g in August 1968, weighed 930 g that November, and 800 g in January 1969; the following August its weight was 975 g. Almost a year later, in July 1970, it weighed 1 025 g.

Animal No. 479 weighed 635 g on July 12, 1968; 850 g on July 19, 1969; 875 g on the 28^{th} of the same month. The identical weight, 875 g, was recorded twice more, the last time on July 18, 1970.

Animal No. 700 weighed 575 g in August 1968. By November its weight was 670 g, but a month later it was down to 535 g. Four weights obtained during the summer of 1969 ranged from 630 to 720 g. In May 1970, this individual weighed 725 g. On August 21, 1970 it had increased to 800 g.

Animal No. 253, with an initial weight of 1 120 g in July 1968, weighed only 100 g more in August 1971. Its lowest weight was 980 g in January 1969 and its greatest weight was 1 250 g in August 1970.

Animal No. 257, with an initial weight of 635 g in June 1968, increased to 1 090 g in June 1969. A month later its weight dropped to 975 g. In July 1971 it weighed 1 100 g.

Animal No. 727 weighed 620 g in August 1968. In May 1969 it had increased to 730 g and a year later, August 1970, to 875 g. Its final weight showed a decline to 790 g in July 1971.

Only 7 individuals with an initial weight less than 200 g were recaptured more than 3 months after marking. These small animals occur in crevices where they easily escape detection, although even here they are not abundant. (The argument that they really are common but extremely hard to find is intrinsically incontrovertible, but, from what searches we have made, seems unlikely.) Data from these recaptures are given in Table 2.

Table 2

Growth data for small *Cryptochiton stelleri*

Identification Number	Initial Weight (g)	Initial Date	Final Weight (g)	Final Date
RBBR	50	24 July 1964	115	15 May 1965
575	50	8 August 1968	75	16 January 1969
553	100	27 July 1968	170	16 January 1969
RRRG	121	27 July 1964	171	18 December 1964
BBRR	123	10 July 1964	188	15 May 1965
722	130	9 August 1968	130	3 May 1969
GGYR	153	27 July 1964	194	20 November 1964

During the field observations, seasonal differences in the animals' behavior were evident. From late October to April even the large chitons were less conspicuous. Then they usually could be found adhering tightly to the substratum or to large, loose boulders. Individuals were not seen actively feeding during this time, whereas in later spring and in summer feeding was often observed. Changes in weight tend to support the idea that *Cryptochiton* here fast during the winter, probably because of a relative paucity of larger algae but perhaps also for other reasons. (These may include turbulence, salinity and turbidity of the coastal water.) Such a cessation of feeding seems not unusual, and apparently also occurs in *Tegula funebralis* (A. Adams, 1855) (see Frank, 1965). Evidence for fasting comes from dissections of *Cryptochiton* in December 1968, and January, February and March 1969, when guts were lacking visible food material; in summer the foregut was often stuffed with millimeter-sized and larger pieces of algae. We do not know whether feeding is so restricted that a real loss in tissue weight occurs. Total weight does decrease at this time, as attested to by numerous short-term weight changes, of which, at this time of year only, the majority are negative (Table 3). The data we have from weighing, dissection, and observations of spawning, indicate that shedding of gametes occurs in June or early July. This may be compared with the observation of Tucker & Giese (1962), who place spawning between March and May among animals occurring some 750 km farther to the south.

Table 3

Percentage of positive short-term (less than 3 months) weight changes in *Cryptochiton stelleri* at different times of year

Month of recapture	Number of recaptures	Percentage showing weight gain
December	33	36.4
January	29	41.4
May	78	80.8
June	24	70.8
July	35	71.4

DISCUSSION

Habitat differences of *Cryptochiton* living in different latitudes raise some interesting questions. Many, though not the majority, of individuals along the Oregon coast range into the low intertidal zone. This is not true farther south,

where subtidally the animals are probably equally abundant. What behavioral elements are involved and whether there is a genetic basis for the difference are not known. It is conceivable that the intertidal animals are those displaced from otherwise more favorable subtidal areas by intraspecific competition. However, there is no evidence whatever for such a supposition. Unfortunately, our data provide insufficient information to make a useful test of the hypothesis that growth rate among intertidal and subtidal animals is the same. The amount of individual variation observed is too great, and it obscures small, systematic differences that may exist. There is the further complication that it is possible and likely that localized populations may have different growth rates. Certainly, size distributions in locales 100 m or more apart differ. Such differences may result from long-term movements or from differences in growth rate. More thorough examinations of differences in size distribution over an area encompassing perhaps as much as 1 km^2 may be required if any real attempt is to be made to trace such differences to even proximate causes.

It is necessary to emphasize that the growth rates observed in Oregon may be exceedingly poor estimates for other areas. This is not the appropriate place for a lengthy discussion of the question of temperature compensation. It would be of considerable interest, however, to have data comparable to ours for, say, the central California coast. Judging from results for *Tegula funebralis* (Frank, in MS), growth rates twice those we have observed would not be inconsistent there. If this should prove true, life spans in the southern part of the range of this chiton quite possibly may not exceed 10 years. Equally interesting would be an examination of growth among these animals farther north.

In the light of our inability to detect unambiguous growth lines corresponding to those seen by the MacGinities (1968), it seems doubtful that comparisons of shell plates from different areas will be sufficiently useful to give clearcut answers to such questions. However, this certainly seems the first place to look.

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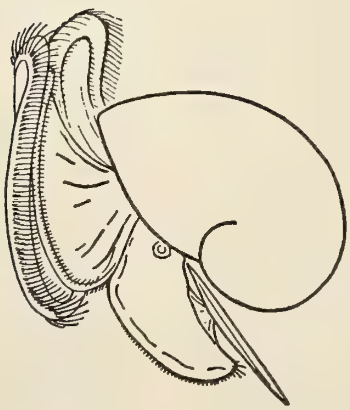

The Taxonomy and Distribution of *Marianina rosea* (Pruvot-Fol, 1930) and *Thecacera pacifica* (Bergh, 1883) comb. nov.

(Opisthobranchia : Dendronotacea and Doridacea)

BY

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DURING 1971 - 1972, NEVILLE AND BARBARA COLEMAN of Sydney journeyed completely round Australia, and, as a side-line to their own particular marine interests, collected and photographed opisthobranch molluscs for the writer. Their collection has since been deposited in the National Museum of Victoria, Victoria, and ultimately a report on the whole collection will be published.

The following notes concern 2 species which are new records for the Australian coastline, and their taxonomy.

Marianina rosea (Pruvot-Fol, 1930)

Under the name *Aranucus bifidus* Odhner (1936: 1091), CARLSON & HOFF, (1973: 172) described and figured living specimens from Guam, and noted its occurrence at Anatahan and Pagan Islands in the northern Marianas. Odhner's type and only specimen came from the lagoon at Aranuka, Gilbert Islands.

PRUVOT-FOL (1930: 229) briefly but adequately described *Mariana rosea* from living animals collected at Île de Pins, New Caledonia. *Mariana* Pruvot-Fol, 1930, being pre-occupied by the nomen nudum *Mariana* Quoy & Gaimard, 1825, she proposed the replacement name *Marianina* (1931: 309). ODHNER (1936: 1077) dismissed *Marianina* as too poorly characterized for inclusion in his magnificent revision of the Dendronotacea, but at the same time (p. 1078) admitted that it might be identical with his *Aranucus*. Later, he fully synonymized *Aranucus* with *Marianina* (ODHNER *in* FRANC, 1968: 874), even changing the family name from Aranucidae to Marianinidae. At species level, the respective types are obviously identical; the species should therefore be known as *Marianina rosea* (Pruvot-Fol, 1930).

In June 1972, Neville and Barbara Coleman collected and photographed 2 lots of *Marianina rosea* at the Blows, Point Quobba, north of Carnarvon, Western Australia (113°25′E; 24°29′S). A single specimen, found under a sponge at 1.2 m depth, had violet body, cream tentacles, foot corners, processes and lobe of rhinophoral sheaths, and red rhinophores. Six specimens, found under coral at 2 m, had mauve bodies darker in the head region, cream distal $\frac{2}{3}$ of tentacles, foot corners, processes and lobe of rhinophoral sheaths, and orange rhinophores. All specimens agree fully with the descriptions of living animals (PRUVOT-FOL, 1930; CARLSON & HOFF, 1973) and preserved material (ODHNER, 1936).

According to the above records, *Marianina rosea* is widely distributed throughout the western Pacific Ocean. Its occurrence in Western Australia is the first record for Australia and the Indian Ocean.

Thecacera pacifica (Bergh, 1883) comb. nov.

One of the *Challenger* opisthobranchs collected in Australian waters was the polycerid *Ohola pacifica* Bergh (1883: 101; 1884: 52). It was discovered in the Arafura Sea. Its most striking features were the 2 pairs of large clavate appendages, one pair level with the rhinophores, the other with the gills. Some years later, ELIOT (1908: 101) identified a Red Sea specimen with this species and gave notes on the living animal. These notes and the description of his preserved animal coincide exactly with that of *Thecacera inhacae* Macnae (1958: 350) from southern Mozambique.

The one difference between the descriptions of *Ohola pacifica* and *Thecacera inhacae* is the shape of the rhino-

phoral appendages. In Bergh's specimen of *O. pacifica* they are described as clavate, whereas the Red Sea and Mozambique specimens have a thin broad appendage folded around the anterior lateral side of each rhinophore. Bergh refers to his specimen as distorted by the picric acid fixative, in which case flaccid rhinophoral appendages would be cylindrical in shape.

The manner in which the under mentioned specimen is preserved in 70% alcohol, with the rhinophoral appendages stout and somewhat cylindrical, confirms Bergh's suggestion of distortion. The 2 genera must be combined, with *Ohola* Bergh, 1883 reduced to a junior synonym of *Thecacera* Fleming, 1828. The species will now be known as *Thecacera pacifica* (Bergh, 1883) comb. nov., with *T. inhacae* Macnae, 1958, as a junior synonym.

In October 1972, Neville and Barbara Coleman collected and photographed a single specimen of *Thecacera pacifica* in 10m at Kendrew Island, off Dampier, Western Australia (116°40′E; 20°41′S). The body was bright orange. The triangular rhinophoral appendages were all black except for a bluish-white stripe along the edge; each appendage had a basal orange crescent-shaped ridge on the outer side as in *T. picta* Baba (1972: 88). The clavate post-branchial appendages were black for the upper $\frac{1}{3}$ with a bluish-white patch on the very top. A black ridge on the tail tip also had a stripe of bluish-white. The rhinophores, 5 gills and the anal papilla were orange with black tips.

Thecacera pacifica is a new record for Western Australia. Its occurrence in the Arafura Sea, Red Sea, southern Mozambique and north-western Western Australia suggests an Indian Ocean rather than Pacific distribution.

ACKNOWLEDGMENTS

The writer wishes to express his gratitude to Mr and Mrs Neville Coleman of Sydney for their invaluable collection of Australian opisthobranchs, and to the Science and Industry Endowment Fund, C.S.I.R.O., Canberra for continuing support of opisthobranch research.

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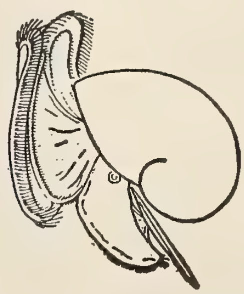

The Ovulidae: A Key to the Genera, and other Pertinent Notes

(Mollusca : Gastropoda)

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INTRODUCTION

THE PURPOSE OF THIS PAPER is to provide keys to the generic units of the Ovulidae and to summarize the history of the ovulid taxonomy. The first major attempt at a classification was by SCHILDER (1927), who later modified this early scheme (SCHILDER, 1932, 1968, 1971). Further modifications were made by CATE (1973), and the present paper suggests a few other needed changes of taxonomic sequence (see Tables 1 and 2). A few supplemental notes on nomenclature and systematics, with some addenda, are also included.

KEY TO THE GENERA OF THE OVULIDAE

My previous paper (CATE, 1973) was an illustrated review of all the named species of Ovulidae. With this material at hand it is now possible to take a more comprehensive view of the family. Examining the morphology, one can recognize better ways to group the various units into a logical sequence. Especially critical is the need of drawing a dividing line between the two tribes, for there is a clinal or transitional change of shell form between Ovulini and Volvini (Simniini) which Schilder did not clearly define. It is my opinion that the straightening out of the shell aperture and the concomitant elongation of the terminal ends provide a good basis for separation into two tribes: the Ovulini are characterized by ovate to globular shells, whereas in Volvini there is a total, or nearly total, lack of a central broadening of the shell.

The key adopted for the Ovulidae is dichotomous and is based upon successive optional dual alternatives. In order to retrace a chosen alternative, the numbers of preceding choices have been added in parentheses at the start of each pair of dual options. As an example, option 1 leads to option 2 or option 3, while the number in parentheses adjacent to 2 or 3 shows that these options were arrived at from choice 1 [see KEEN (1963: 1) for an added explanation of this type of key arrangement].

It should be pointed out that the key does not imply any special sequence of the generic arrangement but has been based upon morphological similarities in the species groups. Numbers in brackets following the genus name refer to plate figures in CATE (1973) which best illustrate the morphologic character of that unit.

During the preparation of this paper I have had the gracious assistance of Dr. Myra Keen of Stanford University, especially in the drafting of the key to the genera. I am deeply grateful to Dr. Keen for this and other guidance. I am also indebted to Jean Cate for constructive suggestions, and to all who have written me their criticisms and praise I wish to express my thanks.

Key to the tribes and subfamilies of the Ovulidae

1. Shell cypraeiform, with incised transverse striation over entire surface; both lips of aperture ribbed 2
   Shell not cypraeiform, transverse striation, if present, not incised; lips of aperture smooth to dentate but not ribbed 3
2. Transverse striation not secondarily sculptured ...... Eocypraeinae, Eocyprini
   Transverse striation pustulose dorsally ...... Jennerini
3. Aperture somewhat curved, shell moderately to markedly inflated ...... Ovulinae
   Aperture narrow, nearly straight; shell mostly narrow in outline ...... Volvini

Key to the genera and subgenera of the Ovulidae

1. Shell cypraeiform, both margins of aperture ribbed 2
Shell not cypraeiform; margins of aperture smooth to dentate 3

2. (1) Sculpture of regular incised striae throughout .... *Pseudocypraea* [1]
Sculpture of dorsum pustulate in adults .... *Jenneria* [2]

3. (1) Shells relatively large (length over 60 mm) 4
Shells small to medium sized (length under 60 mm) 5

4. (3) Ovate, canals short, twisted, especially adapically; outer lip crenulate .... *Ovula* [189]
Spindle-shaped, canals long and slender; outer lip smooth .... *Volva* [245]

5. (3) With broadly truncate terminal ends; shell with medial angulation 6
With ends rounded to pointed, especially adapically; no angulation 10

6. (5) Ends of shell broad; aperture straight, central .... *Cyphoma* [146]
Ends of shell narrowed, aperture curved 7

7. (6) Terminals short; dorsum with a raised knob near ends .... *Calpurnus* [135]
Terminals well developed; dorsum smooth to striate 8

8. (7) Outer lip ridged, but not truly dentate .... *Crenavolva* [101]
Outer lip with projecting teeth, especially adapically 9

9. (8) Angulation with spaced knobs .... *Rotaovula* [100]
Angulation smooth or evenly striate *Dentiovula* [19]

10. (5) Outline nearly globose 11
Outline ovate to elongate 12

11. (10) Outer lip denticulate; dorsum striate .... *Galeravolva* [3]
Outer lip smooth to slightly crenulate: dorsum smooth .... *Globovula* [40]

12. (10) Evenly ovate, *i. e.,* greatest diameter about midway between ends of shell 13
Pyriform (greatest diameter posterior to midline) to elongate 17

13. (12) Outer lip broad; shell weakly striate throughout 14
Outer lip narrow to moderate; striation, if present, mainly at ends 15

14. (13) Aperture curved to left adapically .... *Procalpurnus* [137]
Aperture curved to right adapically .... *Neosimnia* [201]

15. (13) With well developed terminal ridge abapically; outer lip with deeply incised teeth .... *Prionovolva* [14, 16a]
Without (or having a weak) terminal ridge abapically 16

16. (15) Lip teeth weakly developed *Testudovolva* [8]
Lip teeth well developed .... *Sandalia* [191]

17. (12) Spire area flattened; dorsal striation strong, even .... *Carpiscula* [133]
Spire not flattened; striations weak or uneven 18

18. (17) Shell pyriform in outline (greatest diameter adapical to midline) 19
Shell elongate 31

19. (18) Color present in bands, or color spots coalesced .... *Margovula* [27]
Color, if present, not in bands 20

20. (19) Color, if present, in spots .... *Diminovula* [49]
Color not present or uniformly distributed 21

21. (20) Abapical extremity elongate, recurved .... *Lacrima* [35]
Abapical extremity not elongate or recurved 22

22. (21) Lip thin, never reflected 23
Lip broad, reflected 24

23. (22) Outer lip edge thin .... *Xandarovula* [67]
Outer lip edge corded .... *Labiovolva* [65]

24. (22) Terminals short, flattened; shell diameter about $\frac{2}{3}$ of length .... *Inflatovula* [59]
Terminals moderately projecting; diameter less than $\frac{2}{3}$ of length 25

25. (24) Outer lip with sharp denticles 26
Outer lip smooth or weakly dentate 27

26. (25) Terminals spatulate .... *Serratovolva* [111]
Terminals pointed .... *Cuspivolva* [113]

27. (25) Aperture broad, lip thin 28
Aperture narrow, lip moderate to thick 29

28. (27) Dorsum with low angulation .... *Stohleroma* [97]
Dorsum evenly arcuate .... *Aperiovula* [71]

29. (27) Terminals projecting, looped *Pseudosimnia* [44]
Terminals roundly blunt 30

30. (24) Terminals relatively wide; dorsum with a low angulation; aperture curved *Adamantia* [90]
Terminals narrow, evenly rounded *Primovula* [80]

31. (18) Adapical terminal squared at end 32
Adapical terminal slot-like, not squared 33

32. (31) Aperture narrow, almost linear throughout .... *Kuroshiovolva* [200]
Aperture not linear, wider abapically .... *Hiatavolva* [194]

33. (31) Ends attenuated, adapical end pointed, almost needle-like 34
Ends looped or rounded 38

34.(33) Terminals markedly long, tending to be recurved .... *Calcarovula* [239]
Terminals only moderately long, not recurved 35
35.(34) Inner lip longer than outer lip 36
Inner lip not longer than outer lip 37
36.(35) Aperture relatively broad throughout .... *Turbovula* [230]
Aperture narrowed above mid-line .... *Pellasimnia* [220]
37.(35) Terminals long at both ends; outer lip angulate .... *Phenacovolva* [213]
Terminals only moderately long; outer lip thin, not angulate .... *Spiculata* [182a]
38.(33) Funicular ridge strongly spiral 39
Funicular ridge weak or wanting 41
39.(38) Outer lip with a thickened or corded edge .... *Pseudocyphoma* [156]
Outer lip no more than moderately thickened 40
40.(39) Aperture broad for its full length .... *Simnialena* [165]
Aperture narrowed adapically .... *Dissona* [186]
41.(38) Adapical canal broadly looped; columella with a well developed ridge .... *Cymbovula* [181]
Adapical canal not broadly looped 42
42.(41) Outer lip thin .... *Simnia* [157]
Outer lip broad to reflected 43
43.(42) Outer lip strongly dentate; sculpture granose .... *Prosimnia* [162]
Outer lip and shell smooth or nearly so 44
44.(43) Lanceolate, aperture narrow .... *Aclyvolva* [173]
Relatively short; aperture moderate to broad 45
45.(44) Aperture broad .... *Subsimnia* [161]
Aperture of medium width .... *Delonovolva* [124]

History of the Genera of the Ovulidae

With the present expansion of the taxonomic structure of the Ovulidae it appears pertinent at this time to trace the usage of generic names in that group through the years, starting with SCHILDER's (1927) work as the beginning of modern study of the family. Schilder's specialization in the superfamily Cypraeacea, of which the family Ovulidae is an integral part, brought these shells under a more intensive scrutiny, perhaps, than ever before, although the Cypraeidae *sensu stricto* were always his primary interest.

In the past, information about the Ovulidae has been rather obscure for the most part, with almost no radular studies recorded; this has led to much synonymy and to erratic generic assignments. The number of known species has now grown, however, where the terms "splitting" and "lumping" will no longer explain the intra-family relationships in the Ovulidae.

The generic history of the Ovulidae began, in a sense, with LINNAEUS (1758), who used a single genus, *Bulla,* naming 23 species. Only 5 of these, *ovum, volva, spelta, verrucosa,* and *gibbosa* belong to the group we now consider ovulids; the name *Bulla* itself has, through taxonomic processes, been restricted to a group of shelled opisthobranchs.

Next, GRONOVIUS (1781) separated the ovulids from the broader Linnaean group under the name *Amphiperas.* However, in ICZN Opinions 260 and 261 (10 August 1954) the Commission "rejected for nomenclatural purposes the work of Meuschen issued in 1778 under the title *Museum Gronovianum*" (Opinion 260) and "rejected for nomenclatural purposes the Index to the *Zoophylacium Gronovianum* of Gronovius prepared by Meuschen and published in 1781" (Opinion 261).

Gronow did not publish *Amphiperas* and the publication of it by Meuschen was in a non-binomial work. Meuschen's work was accepted for a time; this explains why Schilder used the name in 1927 and 1932 but abandoned it in 1968. HERRMANNSEN (1846) validated *Amphiperas* but only as a synonym of the earlier *Ovula* of BRUGUIÈRE (1789).

SOWERBY [1st] (1828) published a review recognizing this group, listing 24 ovulid species, 13 of which were new to science, under the variant spelling *Ovulum.* KIENER (1843) gave a more formal monographic treatment. SOWERBY [2nd] (1848) and REEVE (1865) used the spelling *Ovulum,* in each case expanding the number of species as discovery at that time warranted. They also began broadening the generic concept by listing limited synonymies, incorporating generic names used by prior authors: *Amphiperas, Calpurnus, Radius,* and a part of the Linnaean *Bulla.* ROBERTS (1869-1870) compiled a catalog but did not attempt special or new generic treatment.

WEINKAUFF (1882) continued the use of the single genus *Ovula,* and like Sowerby [2nd] and Reeve, he listed limited synonymies of the early authors. TRYON (1885) cited the genus *Ovula* without synonymy, though he did use 4 subgenera: *Cyphoma, Volva, Neosimnia, Calpurnus,* and, in error, a subgenus *Crithe* Gould, 1860. *Crithe* is not ovulid in nature and has later been assigned to another molluscan family, the Marginellidae.

SCHILDER (1927), in his work with the Cypraeacea (Cypraeidae, Ovulidae, Triviidae, Eratoidae) began what has since been a slow, steady, systematic structuring of the

ovulid species-groups by grouping together those species having similar shell morphology into a number of generic units with a significantly divergent common shell form; and by further recognizing the importance of locality and distribution details. Also the significance of their racial history (the dimension of time) began to emerge, and using fossil specimens Schilder attempted to establish and list the species in a phylogenetically related sequence (SCHILDER, personal communication).

Although Schilder's work was primarily with the Cypraeidae, he did concern himself with the Ovulidae to the extent of proposing several new tribal and subgeneric names. IREDALE (1930, 1931) contributed 4 new generic names: *Prionovolva, Diminovula, Phenacovolva,* and *Pellasimnia* to accommodate further the expanding concept of the species groups. The following 2 Tables illustrate this development, thus making possible a better visual picture and understanding of the Ovulidae.

Table 1

SCHILDER, 1927	SCHILDER, 1932
AMPHIPERASIDAE	AMPHIPERATIDAE
Eocypraeinae	
Cyproglobina (Cyproglobina)	
Cyproglobina (Pseudocypraea)	
Cypropterina (Cypropterina)	
Cypropterina (Jenneria)	
Amphiperasinae	Amphiperatinae
Amphiperasini	Amphiperatini
Sulcocypraea	
Primovula (Primovula)	*Primovula (Primovula)*
	Primovula (Diminovula)
Primovula (Pseudosimnia)	*Primovula (Pseudosimnia)*
	Primovula (Prosimnia)
	Prionovolva
Calpurnus	*Calpurnus (Calpurnus)*
	Calpurnus (Procalpurnus)
Amphiperas	*Amphiperas*
Simniini	Volvini
Simnia (Simnia)	*Simnia*
Simnia (Prosimnia)	
Simnia (Neosimnia)	*Neosimnia*
Cyphoma	*Cyphoma*
Radius	*Volva*

APPENDED NOTES

The saying goes that the plans for a battleship become obsolete long before the ship's keel has been laid down. The work on the Ovulidae seems analogous in its own development pattern. An example of this is the apparent need to improve the placement of the genus *Dentiovula* by shifting it from near *Prionovolva,* where it was cited in CATE (1973: 13) to the vicinity of *Aperiovula.* One species, cited as *Delonovolva serrula* (*ibid.*, p. 59), seems rather to belong in the genus *Cuspivolva.*

I am retaining the separation of the genera *Phenacovolva* Iredale, 1930 and *Pellasimnia* Iredale, 1931, although it seems difficult to recognize a clear-cut morphological division between them. However, tentative acceptance of the separation is based upon differences in shell characters, as defined in the Key to the Genera above.

HABE (1961: 41) proposed a new genus name, *Dentiovula,* for a markedly dentate group of species, with *Ovulum dorsuosa* Hinds, 1844 as type species; the name was repeated correctly as originally spelled, in the index (p. 151); in the Appendix (p. 14) the name is spelled in a different way, *Dentivolva.* Authors have cited both spellings, but no one seems to have pointed out their equivalence. Therefore, acting as "first reviser" under ICZN Code Art. 32-b I here propose to retain Habe's original spelling, *Dentiovula,* as the correct and valid one, with *Dentivolva* as an objective synonym.

SCHILDER (1927: 70, 80) misspelled the subfamily and tribus names of the genus *Amphiperas*: in SCHILDER (1932: 50, 51) he emended Amphiperasidae to Amphiperatidae, and Amphiperasini to Amphiperatini.

Table 2

SCHILDER, 1968	SCHILDER, 1971	CATE, 1973	CATE, herein
OVULIDAE	OVULIDAE	OVULIDAE	OVULIDAE
Eocypraeinae	Eocypraeinae	Eocypraeinae	Eocypraeinae
Eocypraeini	Eocypraeini	Eocypraeini	Eocypraeini
Pseudocypraea	*Pseudocypraea*	*Pseudocypraea*	*Pseudocypraea*
Cyproglobini	Cyproglobini	Cyproglobini	Jenneriini
Jenneria	*Jenneria*	*Jenneria*	*Jenneria*
Ovulinae	Ovulinae	Ovulinae	Ovulinae
Ovulini	Ovulini	Ovulini	Ovulini
			Ovula
		Galera	*Galeravolva*
		Testudovolva	*Testudovolva*
Prionovolva	*Prionovolva*	*Prionovolva*	*Prionovolva*
		Dentiovula	
		Margovula	*Margovula*
		Lacrima	*Lacrima*
		Globovula	*Globovula*
Pseudosimnia	*Pseudosimnia (Pseudosimnia)*	*Pseudosimnia (Pseudosimnia)*	*Pseudosimnia (Pseudosimnia)*
	Pseudosimnia (Diminovula)	*Pseudosimnia (Diminovula)*	*Pseudosimnia (Diminovula)*
		Pseudosimnia (Inflatovula)	*Pseudosimnia (Inflatovula)*
		Pseudosimnia (Labiovolva)	*Pseudosimnia (Labiovolva)*
		Xandarovula	*Xandarovula*
			Dentiovula
		Aperiovula	*Aperiovula*
Primovula (Primovula)	*Primovula (Primovula)*	*Primovula (Primovula)*	*Primovula (Primovula)*
Primovula (Diminovula)			
Primovula (Prosimnia)	*Primovula (Prosimnia)*		
		Primovula (Adamantia)	*Primovula (Adamantia)*
		Stohleroma	*Stohleroma*
		Rotaovula	*Rotaovula*
		Crenavolva (Crenavolva)	*Crenavolva*
		Crenavolva (Serratovolva)	*Serratovolva*
		Crenavolva (Cuspivolva)	*Cuspivolva*
		Delonovolva	*Delonovolva*
		Carpiscula	*Carpiscula*
Procalpurnus			
Calpurnus	*Calpurnus (Calpurnus)*	*Calpurnus (Calpurnus)*	*Calpurnus (Calpurnus)*
	Calpurnus (Procalpurnus)	*Calpurnus (Procalpurnus)*	*Calpurnus (Procalpurnus)*
Ovula	*Ovula*	*Ovula*	
		Cyphoma	
		Pseudocyphoma	
			Simnia
			Subsimnia
			Simnialena
			Spiculata
			Sandalia
			Neosimnia
			Pellasimnia
			Turbovula
			Cyphoma
			Pseudocyphoma
Simniini	Simniini	Simniini	Volvini
Simnia	*Simnia*	*Simnia*	
Cyphoma	*Cyphoma*	*Subsimnia*	
		Prosimnia	*Prosimnia*
		Simnialena	
		Aclyvolva	*Aclyvolva*
		Cymbula	*Cymbovula*
		Spiculata	
		Dissona	*Dissona*
		Sandalia	
		Hiata	*Hiatavolva*
		Kuroshiovolva	*Kuroshiovolva*
		Neosimnia	
	Phenacovolva (Phenacovolva)	*Phenacovolva (Phenacovolva)*	*Phenacovolva*
Pellasimnia	*Phenacovolva (Pellasimnia)*	*Phenacovolva (Pellasimnia)*	
		Phenacovolva (Calcaria)	*Calcarovula*
Volva	*Volva*	*Volva*	*Volva*
Volva (Phenacovolva)			

Schilder regarded *Jenneria* Jousseaume, 1884, as a subgenus of *Cypropterina* Gregorio, 1880, and therefore relegated the tribus name Jenneriini Thiele, 1929, to the synonymy under his later Cyproglobini. However, recent authors accept *Jenneria* as a full and separate genus, a ranking with which I concur. There remains, then, no reason for continuing to disregard Jenneriini, which has 3 years' priority over Cyproglobini Schilder, 1932, and I have recommended that it be reinstated.

In Schilder (1968: 272) the generic name *Volva* Röding, 1798, seems to have been inadvertently omitted. It should appear as line 14 of column 1, page 272, and the present line 14 should move to line 16, the present line 16 then being superfluous. It would also seem that the genus *Primovula* Thiele, 1925 (Schilder, *op. cit.*: 271), should be moved up and inserted just above *Diminovula* Iredale, 1930, for *Diminovula* is indicated as a subgenus of *Primovula.*

ADDENDA to Cate, 1973

Included here are errors and omissions discovered after the printing of this work was completed: on page IV, add: NM – Natal Museum, Pietermaritzburg, South Africa; on page 1, in the 4th paragraph of the introduction, the citation Schilder & Schilder (1971) refers to: A catalogue of living and fossil cowries - taxonomy and bibliography of Triviacea and Cypraeacea (Gastropoda Prosobranchia). Mém. Inst. Roy. Sci. Nat. Belg. (2) 85; and Wilson & Gillett (1972:62; plt. 44, fig. 8) refers to: Australian Shells. Charles E. Tuttle Co., Vermont & Tokyo, Japan; pp. 1 - 168; plts. 1 - 106; 34 text figs.

On p. 3, column 2, line 7, read: Binder, MHN;

p. 4, column 1, line 2, read: BUMO (not BUMC)

p. 4, column 1, lines 3 & 4, read Habe, NSMT and Kosuge, NSMT

ibid., line 11, read: James H. McLean

p. 10, column 1, line 6 from bottom, correct name to: [cf. *Primovula (Primovula) dautzenbergi*]

ibid., line 12, read: *Primovula (Adamantia) concinna*

p. 11, column 1, line 17: correct *Prionovolva frutica frutica* (Reeve, 1865) to *Prionovolva pudica pudica* (A. Adams, 1854)

p. 11, column 2, line 10, correct *Prionovolva caledonica* to *Pseudosimnia (Diminovula) caledonica*

ibid., line 21 read: (see listing of *P. pudica pudica*

p. 23, column 1, line 12, correct genus name from *Globovula* to *Prionovolva (bulla)*

p. 24, column 1, line 11, read: *Ovulum umbilicatum* Sowerby 2nd, 1848

p. 24, column 2, line 13, correct date 1800 to 1900

p. 24, species 42, line 2 of synonymy should read: *Ovula dentata* Fischer (von Waldheim)

p. 29, column 2, species 53, add parentheses to (Duclos, 1831)

p. 30, column 2, line 15, add to the discussion: I am naming this new species in honor of the late Archer Whitworth, of Geraldton, West Australia, who contributed much to our knowledge of the Cypraeacea of that area.

p. 40, column 1, species 76, correct date in synonymy, *beckeri* Schilder, from 1841 to 1941

p. 43, column 2, line 20, correct *Pellasimnia* to *Prosimnia verconis* ...

p. 46, column 2, line 2, correct *P. (A.) fulguris* to *Pseudosimnia (Diminovula) fulguris* Azuma & Cate, 1971

p. 46, column 1, line 8 from bottom, read: NSMT

p. 52, column 1, line 2, the author's name should read Fischer (von Waldheim)

p. 79, column 2, line 3 from the bottom, read: *Aclyvolva clara* Cate, 1973;

p. 82, column 1, line 25, correct *Simnialena* to *Cymbula acicularis*

p. 87, column 1, line 13, correct *praenominate* to *praenominata*

p. 87, column 2, line 12: instead of 22 (4): ... read 11 (4): ...

pp. 92 and 93, correct date on *Phenacovolva* Iredale from 1939 to 1930

p. 94, species 184, correct name to *Phenacovolva (Phenacovolva) rosea lahainaensis*

p. 96, column 2, line 14 correct date from 1843 to 1848

on pp. 96, 99, 108, remove parentheses from the authors' names and date [Azuma & Cate, 1971]

p. 105, column 1, line 4 from bottom read: 8 March, 1933

p. 111, column 2, line 2 from bottom, read: NSMT

p. 112, column 1, bottom line, correct: *(striatus)* to *(semistriatus)*

In the Index the following corrections are needed:

p. 115, column 2, line 32, correct author's name to Fischer (von Waldheim)

p. 115, column 3: *formosa* (Verco), correct page reference from 52 to 42

p. 115, column 3: *formosa* (A. Adams & Reeve), delete page reference 52

p. 115, column 3, add new reference: *formosa* (Schilder) 50

p. 116, column 1, line 16, correct *nigeria* to *nigerina*

ibid.: after *nigerina* add: *nigerrima* [Tryon, err.] 49

p. 116, column 1, *ovum,* add page reference 36 (species 66: line 2 of Discussion)

Synonymic Reassignments

p. 60, species 122, add to synonymy:
1969 *Simnia aequalis vidleri.* Cate, The Veliger 12 (1): 100

p. 76, species 150, add, after line 23:
1971 *Primovula inflexa.* Cate, The Veliger **13** (4): 363

p. 85, column 1, after line 7, add:
1969 *Volva maccoyi.* Cate, The Veliger **11** (4): 365
1969 *Volva (Phenacovolva) exsul.* Cate, The Veliger **11** (4): 365

p. 87, species 170, after line 17, add:
1971 *Primovula depressa.* Cate, The Veliger **13** (4): 362

p. 96, species 187, add:
1971 *Phenacovolva recurva.* Cate, The Veliger 13 (4): 363

p. 97, species 189, add:
1971 *Phenacovolva angasi.* Cate, The Veliger 13(4): 363

p. 98, species 190, add:
1971 *Phenacovolva subreflexa.* Cate, The Veliger 13 (4): 363

p. 107, species 210, add:
1971 *Phenacovolva piragua.* Cate, The Veliger 13 (4): 363

p. 108, species 211, add, after line 21:
1969 *Volva (Phenacovolva) birostris.* Cate, The Veliger **11** (4): 364; fig. 3

{Note: the figures in the cited paper were mislabeled in the preparation for reproduction.}

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Comments on Some Pacific Coast Mollusca: Geographical, Ecological, and Chronological

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(1 Plate)

This the third of a series of papers (Talmadge, 1972, 1973) in which information is presented pertaining to the geographical range, the ecological biome, and the chronological distribution for certain species of marine Mollusca inhabiting the offshore waters of northern California. In the present discussion I thought it advisable to include some comments or data, or both, obtained from outside my study area which may clarify some of the information presented from within the basic study region. The boundaries of this area are based upon the fishing grounds utilized by the commercial dragboat fleet operating out of Humboldt Bay on the northern California coast. These boats normally fish between the submerged Noyo Canyon, off Fort Bragg, Mendocino County, California, north to off Mack Arch, just north of Brookings, Curry County, Oregon, or between 39°30′ and 42°15′N latitudes. Fossil deposits, dating from Upper Miocene to Upper Pleistocene, are found on the adjacent mainland, and these deposits of the "Wildcat," *sensu lato,* contain faunas similar to or identical with the Recent offshore benthic faunas and consist of strata similar to or identical with the substrata from which our Recent benthic fauna is obtained.

In addition to the material accumulated from the dragboat fleet, I have been given permission to include data obtained from tows made by both the Geology and the Biology Departments of Humboldt State University, Arcata, California. Their dredging was carried out in several transects off the mouth of Little River, Humboldt County, California, or offshore from the Crannell Junction Deposit of Late Pleistocene time, at approximately 40°55′N Lat., at a depth of about 550m, well within the boundaries of the study region. No additional species were obtained by these tows, but the specimens increased the data on several of the more uncommon species.

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The following comments are presented in the hope that they will be of use and interest not only to malacologists, but also to paleontologists, paleoecologists, and ecologists working with Recent species.

BIVALVIA

Macoma elimata Dunnill & Coan, 1968

Recently, Dr. Eugene Coan examined the Recent as well as the fossil specimens of *Macoma* in my collection and verified my identification of *M. calcarea* (Gmelin, 1791) and *M. elimata.* The northern *M. calcarea* is not present in our local Recent fauna, but *M. elimata* has been taken on sandy substrate at approximately 91m off Eureka, California (Lat. 40°45′N).

Martin (1916) had divided the "Wildcat" fossils into a "Lower" and an "Upper" fauna, and I likewise, had found a distinct faunal change or break in the middle of Ogle's (1953) Pliocene Rio Dell Formation. It was interesting to note that the break in the faunas coincided with the separation of the 2 species of *Macoma, M. calcarea* and *M. elimata.* I noted that *M. elimata* was found only in the Upper Wildcat, and *M. calcarea* was restricted to the Lower Wildcat. The fauna of the Lower Wildcat indicated a cold or deep water fauna, or both, consisting of genera represented in our Recent fauna, but with species no longer present. In contrast, the Upper Wildcat fauna consisted chiefly of both genera and species commonly obtained in our Recent molluscan populations at depths of less than 180m.

Fossil specimens of *Macoma elimata* appeared to be restricted to a sandy siltstone, which corresponds to the sandy mud substrata from which Recent specimens were obtained. Fossil specimens of *M. calcarea* were found in a broken, brittle, calcitic mudstone, which appears to

be the same hard blue mud of the offshore substrate but which does not contain Recent *M. calcarea*. As far as I can determine, no specimens of either *M. calcarea* or *M. elimata* have been obtained from the Pleistocene Crannell Junction or Moonstone Beach sites. However, both of these localities contain a fauna chiefly associated with inshore deposits of near subtidal depths.

It appears that during Lower Wildcat time, *Macoma calcarea* was present on a blue mud substrate in association with *Beringius, Plicifusus,* and *Bathybembix*. In Upper Wildcat time, as the waters became more shallow and a sandy mud substrate became common, *M. elimata* replaced *M. calcarea,* although it still persists at suitable depths and in the proper substrate.

Solemya johnsoni Dall, 1891

This interesting and little known clam is represented by 3 categories of specimens: Pliocene fossils, Pleistocene fossils, and Recent examples, all from within the boundaries of the study area. A series of Recent specimens was obtained by Humboldt State University from off the mouth of Little River, Humboldt County, California, at a depth of about 550 m, and I have a small series taken by the M. V. *Ina* from off a green mud substrate in 732 m, obtained in a tow off Trinidad, Humboldt County (Lat. 41°10′N). Specimens were compared with identified material in the Stanford University Collection, Stanford, California and with similarly identified specimens in the collection at the California Academy of Sciences, San Francisco, California. All proved to be *Solemya johnsoni* Dall.

Off Eureka, California at depths between 183 and 366 m, the nets of the dragboats catch onto protruding loose clumps of fossiliferous calcitic rock, apparently from a major deposit sunken below the sand and mud of the sea bed. The fossil fauna of these rocks is so similar that a single deposit appears to be indicated. The matrix is not quite consolidated, and the fauna is identical with Recent material from depths of 550 m. With this information, several local geologists, including myself, consider this deposit to be probably late Pleistocene in age. Two specimens of *Solemya johnsoni* have been obtained from chunks of rock brought in by local dragboats.

Martin (1916), Stewart & Stewart (1949), and Ogle (1953) recorded *Solemya ventricosa* Conrad, 1849, described originally as a Miocene fossil from the Astoria Formation, from various localities within the Pliocene Wildcat Group. Martin (*op. cit.*) recorded his material from the "Lower Wildcat" along the Eel River at Rio Dell, and the "Bear River Miocene." This last locality is on the southern dipping exposure of the generalized Centerville Sea Cliffs, on both the north and south side of False Cape, Humboldt County, the seaward point of a large anticline. Stewart & Stewart (*op. cit.*) list *S. ventricosa* from well down in the lower portion of the Centerville Section, or on the north side of this same anticline, and only a short distance from Martin's site. Ogle (*op. cit.*) gives an Elk River, Humboldt County, location, which is now covered with a deep layer of silt deposited by the 1964 flood, but one item presents an indication on which identifications may be made. This is an association with *Lucina* and *Thyasira,* two bivalves uncommon throughout the Wildcat faunas.

Specimens collected at what may be Martin's Eel River site and specimens taken low down in the Centerterville Sea Cliffs do not agree in shell characteristics with either the Recent or fossil offshore material; neither do they appear to be quite the same as the Miocene Astoria *Solemya ventricosa*. A chance remark by Dr. Warren O. Addicott, U. S. Geological Survey, as to the location of the umbos, had sent me north to Yaquina Bay, Oregon, where I obtained a small series of the Miocene species. With the 4 lots in front of me I began a series of measurements to see if any basic pattern could be observed.

I found a gradual, persistent difference in the length/width ratio of the calcareous portion of the shell, plus a second separation in the placement of the umbo in relation to the length of the shell. Some specimens, of course, failed to fit into any given group, but on the average the ratios were very close. They are presented here only as averages. Miocene specimens from the sea cliffs south of Yaquina Bay, Oregon, have a length/width ratio of 100:39, and the umbos divide the shell into 2 units, 35:65. Specimens from the Pliocene Eel River and Centerville deposits have a length/width ratio of 100:33.2, and an umbo separation of 33:67. The offshore Pleistocene material is measured at 100:31.5 and an umbo ratio of 30:70. Recent specimens exhibit a slightly narrower shell (the periostracum does not fossilize, so only the calcium carbonate shell was used), with a ratio of 100:29 and the division by the umbos at 29:71.

From the above listed data it appears that the early writers had fossil material from the Wildcat of Humboldt County, more similar to the Miocene *Solemya ventricosa* than to the Recent *S. johnsoni* but did not have specimens from what appears to be Pleistocene offshore deposits. This last mentioned material appears to be the key to the gradual change in time from *S. ventricosa* to *S. johnsoni*. Unfortunately, *Solemya* are known as fossils from only a few localities, and even Recent specimens are not too common. Perhaps in due time, as additional material becomes available from research dredging, and as more fossil material is found, a clearer understanding of the evolution of this interesting genus from Oligocene time to the Recent will be obtained.

Solemya panamensis Dall, 1908

Dall (1921) lists the range of this species as from Santa Barbara to Panama; Keen (1937) gives the geographical range in degrees of latitude, from 8° N to 37° N, with a midpoint at 22° N. I could find no records for more northern localities, nor could I obtain data on the ecology except that the species lives in deeper water.

In the early summer of 1970, Captain James Riley of the M. V. *Ina,* while fishing off Trinidad, California (Lat. 41°10′N) obtained a specimen of a small *Solemya* which I was unable to identify to my satisfaction. The single specimen appeared to match the figures and descriptions of *Solemya panamensis,* but I considered that this identification was impossible based upon the published data available to me. I considered that this might be a juvenile *S. johnsoni,* but the physical characteristics of the shell as well as the periostracum, together with the size of the shell made this identification also improbable. Later that summer I had the opportunity to make direct comparisons with specimens identified as *S. panamensis* in both the Stanford University Collection and the collection at the California Academy of Sciences. As far as I could determine, the Trinidad specimen was the same species as the specimens identified as *S. panamensis* in these collections. This northern specimen was taken in 550m, on a soft green mud substrate. At the present time I have not noted the species in any material brought up in the tows made by Humboldt State University; however, juvenile specimens of *S. johnsoni* were obtained in these tows, specimens of a size similar to that of the *Ina* specimen. This rules out a juvenile shell.

GASTROPODA

Amphissa bicolor Dall, 1892

Keen (1937) lists the range of this small gastropod from 33° N to 38° N Lat., with the midpoint of the range at 35° N. Dall (1921) cites the range as from "The Farallones Islands south to San Diego, in deep water." During the late spring and early summer of 1972 several dragboats fishing on a sandy substrate just south of the submerged Eel Canyon off False Cape, California (Lat. 40° 15′ to 40°25′N) dredged up several specimens of this more southern snail. A special search was made for the species from similar habitats and depths (91m), both north and south of this one area, but with negative results. Perhaps there is a warmer isothermic condition at this one locality, compared to certain warmer areas within the intertidal levels which support locally isolated and restricted populations of more southern species. I refer to certain coves cutting into the marine terrace at Point Delgado - Shelter Cove on the Humboldt - Mendocino County boundary at Lat. 40°01′ N. Here one finds a small population of *Pseudomelatoma torosa* (Carpenter, 1864) in one cove and *Fusinus harfordi* (Stearns, 1871) in another separate indentation along the sea cliffs. In both instances the temperature of the water is slightly higher than that of the adjacent open sea. The local discovery of this species extends the geographical range more than 2 degrees northward.

Genus *Colus* Röding in Bolten, 1798

In an earlier paper (Talmadge, 1972) I briefly discussed 2 species of *Colus, C. tahwitanus* Dall, 1918, and *C. halli* (Dall, 1873). Additional specimens of *Colus,* both Recent and fossil, now indicate a much richer fauna of this genus than previously assumed. I now have found 5 species of *Colus* inhabiting the study area, 3 of which are taken both as fossil as well as Recent specimens.

I considered, and still hold the same opinion, that *Colus tahwitanus* is the most common species within this area. Previously I had noted that although the species was found as a Recent shell, no fossil records were available from within the boundaries of the study area. In 1972, the M. V. *Admiral King* netted a large fossiliferous rock from a depth of 329m) from off Eureka, California (Lat. 40° 45′N), and, upon breaking the rock apart, a fine example of *C. tahwitanus* was obtained. This places the species along the northern California coast in Pleistocene time.

Stewart & Stewart (1949) listed *Colus halibrectus* (Dall, 1891) from the Centerville Beach section of the Wildcat Group, but Faustman (1964) considered this to be *C. jordani* Dall, 1913. In this identification I follow Dr. James McLean (personal communication) and consider *C. jordani* to be one of the many synonyms of *C. halli* (Dall, 1891). At the present time I have collected 2 species of *Colus* from the Centerville Sea Cliffs. One is *C. halli,* taken in some numbers just north of Fleener Creek in association with *Antiplanes, Exilioidea, Oenopota, Rectiplanes,* and *Trophonopsis.* The strata at this locality form a massive sandy mudstone. The species is also represented in my collection by one adult Recent live-taken specimen, collected on a soft green mud substrate at 360m, and a dead shell taken in the same tow from off the submerged Eel Canyon. This location is just offshore from the Centerville Sea Cliffs.

In a stratum filled with broken siliceous spicules, many of which had the fused 6-pointed form of the Hyalospongiae, south of Fleener Creek, I found a second species of *Colus, C. halidonus* Dall, 1919. Recent specimens of this species are taken with the massive siliceous sponge,

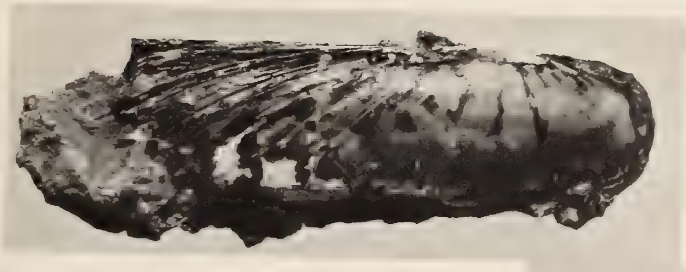

Figure *1*: *Solemya johnsoni* Dall, 1891
off Eureka, from fossiliferous rock

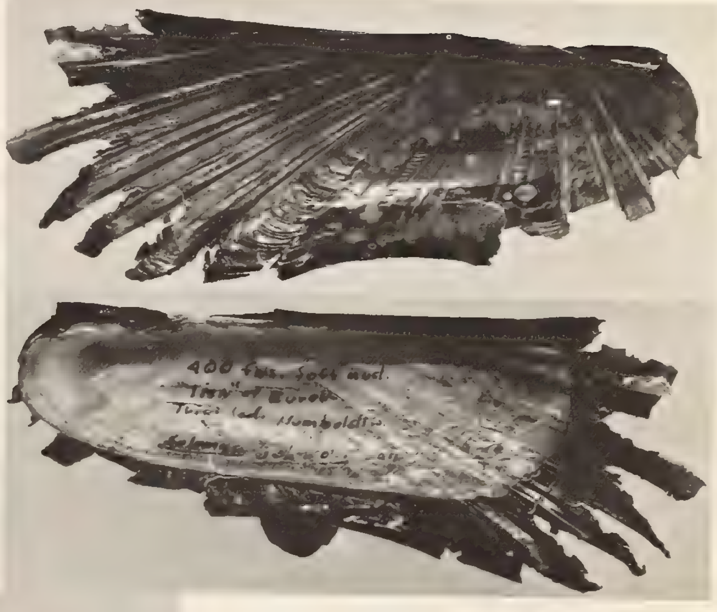

Figure *2*: *Solemya johnsoni* Dall, 1891
off Trinidad, Humboldt County, California
from 732 m; exterior and interior of valves

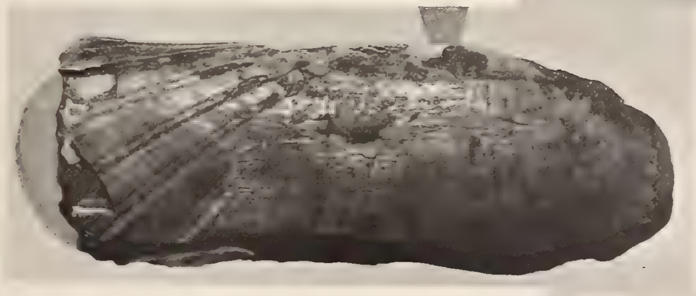

Figure *3*: *Solemya ventricosa* auct.
Middle Rio Dell Formation (Pliocene)
Eel River at Rio Dell, Humboldt County

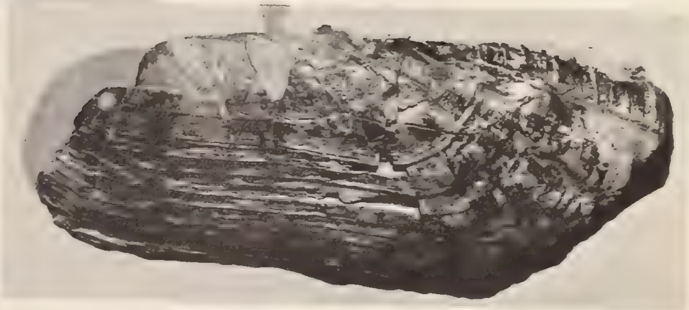

Figure *4*: *Solemya ventricosa* Conrad, 1849
Astoria Formation (Miocene)
Sea Cliffs, S. Yaquina Bay, Oregon

Aphrocallistes vastus Schulze at a depth of 732 m. The *Colus* attaches its egg capsules on this sponge.

Colus severinus (Dall, 1919) has been obtained twice, both times from deep tows at 732 m, on soft green mud off the Centerville Sea Cliffs. Rokop (1972) records *C. dimidiatus* Dall, 1919 from a depth of 3000 m from off Eureka. I have a single specimen of the latter species, taken on green mud at a depth of 915 m at the submerged Eel Canyon, off the Centerville Sea Cliffs.

Mohnia frielei (Dall, 1891)

Previously, my only specimen of this species had been found in a mass of siliceous sponge dredged from 660 m off Mack Arch, Curry County, Oregon (Lat. 42°15′N), the northern limit of the study area, presumed to be the southernmost recorded locality for this species. An additional specimen of *Mohnia frielei* has now been obtained by the M. V. *Claremont*, taken at a depth of 780 m on, or just south of, the Gorda Escarpment (Mendocino Fracture Zone), Lat. 40°20′N. The bottom at this locality is a mixture of green mud and black volcanic sand. This record extends the range of the species one degree southward and confirms mud as a habitat as given by Bernard on the datum of a suite of shells in the collection of the California Academy of Sciences, taken off the west coast of Vancouver Island, Canada.

Neptunea phoenicea (Dall, 1891)

A series of both juvenile and adult specimens of this *Neptunea* was taken at a depth of 550 m off the mouth of Little River, Humboldt County, California (Lat. 40°55′ N). These were obtained by tows made by Humboldt State University science classes. My own records for the occurrence of this species in the study area are all based upon juvenile specimens, with a single adult record from off Point Saint George, Del Norte County, California (Lat. 41°55′N).

Thais lamellosa (Gmelin, 1791)

Most malacologists, myself included, had known that *Thais lamellosa* was not restricted to the intertidal levels but also inhabited submerged rocky reefs to an undetermined depth, which varied, probably for reasons of both food and environment. A search of the literature available yielded a single record of depth, as Rice (1968) stated: "One interesting record is from 65 fms. off Cape Flattery, alive (Duggan)." In late 1972 the crew of M. V. *Admiral King* brought me 3 specimens of *T. lamellosa* which they had picked up from amid the debris of a tow made between 64 and 91 m, on a coarse gravel substrate off Eureka, California. The specimens were compared with adjacent populations from False Cape, the jetties at the entrance to Humboldt Bay, and from a rip-rap near the entrance to Humboldt Bay, and could not be separated from these populations except by the inked catalog numbers on the shells.

AMPHINEURA

In late February 1973, the M. V. *Claremont* returning from San Francisco to Eureka made a tow in 475 m off Point Arena, Mendocino County, California (Lat. 37° 57′30″N) south of the normal study area. Several large boulders were caught in the net and eventually arrived in Eureka. On one of these rocks I discovered 2 chitons and a scaled sea cucumber, *Psolus fabrici* (Düben). The 2 chiton species are rare enough to warrant comment.

Ischnochiton retiporosus (Carpenter, 1864)

A single adult specimen was obtained from a small crevice-like cavity on one of the rocks. There was nothing unusual about the specimen, and the locality is well within the published range of the species. It is mentioned here to add to the recorded data of the species.

Placiphorella pacifica Berry, 1919

In another small cavity of the rock a specimen of this rather strongly sculptured white *Placiphorella* was found still alive. The specimen was placed into fresh sea water, but it did not become active. However, color slides and black and white photographs were made of the unusual specimen as it slowly moved about on a rock placed in the water. The specimen survived for one day and was found dead in the marine aquarium the next day. Again, this record is offered to supplement existing data.

ACKNOWLEDGMENTS

The men of the commercial dragboat fleet operating out of Humboldt Bay, California have made this study possible by their cooperative efforts, obtaining specimens, furnishing data as to depth and substrate and precise collecting localities. To each and all of them I express my sincere appreciation.

I also wish to express my appreciation to Drs. Frank Kilmer and Jack Yarnall of Humboldt State University for permission to use the data on specimens obtained

by that institution. As in past discussions on this same study, I again express my thanks to Drs. A. Myra Keen, Eugene V. Coan, James H. McLean, and the late Dr. Leo G. Hertlein, all of whom encouraged this study and assisted in the identification of certain species. Mr. Allyn G. Smith of the California Academy of Sciences continued his assistance in the identification of the lesser known chitons. To each and all of these persons I can only say "Thank you."

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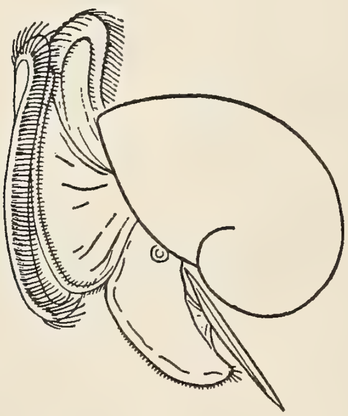

Type and Other Cephalopods in the Collection of the Department of Invertebrate Zoology, California Academy of Sciences

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THE COLLECTION OF PRESERVED INVERTEBRATES formerly housed in the Natural History Museum, Stanford University, Stanford, California, contained about 300 lots of cephalopods. These were left at Stanford when the main collection of invertebrates was transferred to the California Academy of Sciences Department of Invertebrate Zoology, San Francisco, California, in 1963; they were moved to the Academy early in 1971.

This collection dates back to before the turn of the century and contains specimens collected by such well-known zoologists as David Starr Jordan, John O. Snyder, Albert W. C. T. Herre, Edwin C. Starks, Barton W. Evermann, Harold Heath, Olaf P. Jenkins, Walter K. Fisher, and Edward F. Ricketts as well as other later collectors. It is a most important one taxonomically as it formed the basis for a considerable part of the systematic work on the Cephalopoda published by S. S. Berry of Redlands, California, beginning in 1909, especially that relating to the cephalopods of western North America, the Hawaiian Islands, Japan, and the Kermadec Islands.

In spite of the age of many of the specimens in the Stanford Collection, the state of preservation, for the most part, is good. All of them have been re-curated following the California Academy's Department of Invertebrate Zoology standards and now are stacked systematically on collection-room shelves except for types, which are maintained in a separate collection.

As a total of 26 primary type specimens (8 holotypes, 16 paratypes, 2 syntypes) are included in the collection, it seems desirable to provide a list of them for the permanent reference of workers in this class of the Mollusca. In order to make this list as useful as possible, I have included 53 secondary types. These have been designated as hypotypes and represent specimens for which more or less complete measurements, or illustrations, or both, have been published in addition to other descriptive data and information relating to the particular species.

In addition to types and other Stanford specimens, which have been recorded in the literature, I have included for the record 2 paratypes of *Berryteuthis anonychus* (Pearcy & Voss, 1963), a hypotype of *Dosidicus gigas* (d'Orbigny, 1835), and a paratype of *Abraliopsis felis* McGowan & Okutani, 1968. These have been acquired from other sources. All type specimens listed are accessioned and numbered in the California Academy's Invertebrate Zoology Type Series.

TALMADGE (1967) mentions certain other cephalopod specimens in the main Invertebrate Zoology Collection and SMITH (1971) records the acquisition of 2 specimens of *Vampyroteuthis infernalis* Chun, 1903.

The following abbreviations are used:

CASIZ California Academy of Sciences Department of Invertebrate Zoology, general collection, or separate Type Series. No accession numbers are assigned to specimens lots in the general collection as they are shelved systematically for convenient reference.

SSB A series of author's register numbers maintained by Dr. S. S. Berry separately from accession numbers assigned to specimens in his private mollusk collection. SSB numbers represent specimens or specimen-lots seen and studied by him although not necessarily deposited in his own collection.

USNM National Museum of Natural History, Division of Mollusks, Washington, D. C.

For quick inspection the primary types are listed below. These are treated in more detail, together with the secondary types and other specimens, in the subsequent systematic listing.

Family	Species	Type	CASIZ No.
	COLEOIDEA		
Sepiidae			
	Sepia formosana Berry, 1912	Holotype	465
Sepiolidae			
	Euprymna scolopes Berry, 1913	Paratypes (3)	497 - 499
	Rossia pacifica Berry, 1911	Paratypes (2)	495, 496
	Rossia pacifica diegensis Berry, 1912	Syntypes (2)	457, 458
	Sepiolina nipponensis (Berry, 1911)	Holotype	459
	TEUTHOIDEA		
Loliginidae			
	Loligo opalescens Berry, 1911	Holotype	547
	Lolliguncula panamensis Berry, 1911	Holotype	537
		Paratype	538
Cranchiidae			
	Liocranchia globulus Berry, 1909	Paratype	520
Enoploteuthidae			
	Abraliopsis felis McGowan & Okutani, 1968	Paratype	310
	Watasenia scintillans (Berry, 1911)	Holotype	453
Gonatidae			
	Berryteuthis anonychus (Pearcy & Voss, 1963)	Paratypes (2)	23, 24
	Berryteuthis magister (Berry, 1913)	Holotype	463
	OCTOPODA		
Opisthoteuthidae			
	Opisthoteuthis californiana Berry, 1949	Holotype	548
Octopodidae			
	Octopus dofleini apollyon (Berry, 1912)	Paratype	461
	Octopus californicus (Berry, 1911)	Paratype	460
	Octopus gilbertianus (Berry, 1912)	Paratype	510
	Octopus oliveri (Berry, 1914)	Paratype	464
	Octopus pricei (Berry, 1911)	Holotype	454
		Paratypes (2)	455, 456

CEPHALOPODA

COLEOIDEA

Sepioidea

Sepiidae

Sepia aculeata d'Orbigny & Férussac, 1834. Berry, 1912c: 418.

There were no hypotype specimens of this species in the Stanford collection. Others now in the CASIZ collection include the following:

SSB No. 360. A large male from Tsuruga, Echizen, Japan; David Starr Jordan and John Otterbein Snyder, collectors; 1900

Sepia esculenta Hoyle, 1885. Berry, 1912c: 418-419.

No hypotypes in the Stanford collection. The CASIZ Collection contains:

SSB No. 360. A single female from Tokyo, Japan; Jordan & Snyder, coll.; 1900

Sepia formosana Berry, 1912c: 420-422; plt. 9, fig. 7; text fig. 2.

Holotype. CASIZ No. 465 [SSB No. 361]. From

Formosa (Taiwan), Takao fishmarket; Hans Sauter, coll. (no. 5456), 12 January 1907. Based on a single specimen for which measurements are provided (pp. 421-422). OKUTANI (1967: 4) places *S. formosana* in synonymy of *S. pharaonis* Ehrenberg, 1831

Sepia hoylei Ortmann, 1888. BERRY, 1912c: 419-420.

No hypotypes in the Stanford Collection. Other specimen-lots now in the CASIZ Collection include:

SSB No. 356. From Nagasaki, Hizen, Japan; Jordan & Snyder, coll., 1900; 3 specimens from an original series of 4. SSB No. 379. From Wakanoura, Kii, Japan; Jordan & Snyder, coll., 1900; a single juvenile. OKUTANI (1967: 4) indicates *S. hoylei* to be a synonym of *S. esculenta* Hoyle, 1885

Sepia kobiensis Hoyle, 1885. BERRY, 1912c: 423.

No hypotypes in the Stanford Collection. Other material now in the CASIZ Collection, all from Japan, see Table 1.

Sepia tokioensis Ortmann, 1888. BERRY, 1912c: 423.

No hypotypes in Stanford Collection. A single lot, mentioned by Berry, is now in the CASIZ Collection:

SSB No. 377. 3 specimens from Aomori, Mutsu, Japan; Jordan & Snyder, coll., 1900

SEPIOLIDAE

Euprymna morsei (Verrill, 1881). BERRY, 1912c: 408-414; plt. 6, figs. 1, 2.

Hypotype. CASIZ No. 569 [SSB No. 290]. A measured male (p. 412) from an original series of 3 specimens collected at Takao, Formosa (Taiwan), by Hans Sauter

Hypotype. CASIZ No. 570 [SSB No. 291]. A measured female from Japan, specific locality not given, probably Jordan & Snyder coll., 1900

Hypotype. CASIZ No. 571 [SSB No. 292]. A measured female from a series of 3 taken at Onomichi, Bingo, Japan, by Jordan & Snyder, 1900

Hypotype. CASIZ No. 572 [SSB No. 294]. A measured male from a series of 3 taken in the Bay of Waka, Kii, Japan; Jordan & Snyder, coll., 1900

Other Stanford specimens now in the CASIZ Collection include:

SSB No. 289. 4 (2 males, 2 females) from Nagasaki, Japan; Jordan & Snyder, coll., 1900.

SSB No. 293. A single female from Wakanoura, Kii, Japan; Jordan & Snyder, coll., 1900

Euprymna scolopes Berry, 1913b: 564-565; 1914a: 312 to 315, plt. 4, figs. 5-8; text figs. 23-26

Paratypes (3). CASIZ Nos. 497, 498, 499[SSB No. 323]. Sexes not determined. Measurements are provided (1914a: 314) for 2 males but it is not certain that either of these is included in the CASIZ paratypes. Locality for the paratypes (a total of 12) is from a surface haul off Kalaupapa Leper Settlement, Molokai, Hawaii; USS *Albatross* (Sta. 3905) coll., 30 April 1902. Holotype is stated to be in USNM (No. 214380 [SSB No. 320])

Hypotype. CASIZ No. 524 [SSB No. 312]. A measured female taken at the surface off Mokapu Islet, Molokai, Hawaii; USS *Albatross* (Sta. 3889) coll., 17 April 1902

Additional material see Table 1

Heteroteuthis hawaiiensis (Berry, 1909): 409, 418; text fig. 2 (as *Stephanoteuthis hawaiiensis*); 1914a: 319-321; plt. 50, figs. 3-8; text figs. 29, 30.

No type or other material has been found in the Stanford Collection. Type locality: trawled in 385 to 733 fms. off Kauai, Hawaii; USS *Albatross* (Sta.-3989) coll., 11 June 1902. Type lot: a single female. Holotype in USNM No. 214311. According to Berry the USS *Albatross* collected fragmentary specimens from 2 additional stations.

Inioteuthis japonica Verrill, 1881. BERRY, 1912c: 405-408; plt. 5, fig. 5.

Hypotype. CASIZ No. 508 [SSB No. 392]. A measured female (p. 407) from 42-45 fms. off Matsushima, Rikuzen, Japan; USS *Albatross* (Sta. 3770) coll., N 41° E, 4.7 mi. from Nagane Saki, off Honshu, 5 June 1900. This specimen was desiccated, even though in alcohol, on transfer from Stanford. An attempt is being made to re-hydrate it with a detergent.

Another specimen, a female [SSB No. 389] from Enoshima, Sagami, Japan, A. Owsten coll., is now in the CASIZ Collection.

Rossia pacifica Berry, 1911c: 591; 1912b: 290-293; plts. 51, 52; plt. 53, figs. 1-4; plt. 54, figs. 1, 5.

Paratypes (2). CASIZ Nos. 495, 496 [SSB No. 21]. From a type lot of 11 specimens. Type locality: Vicinity of Yes Yes Bay, Behm Canal, Alaska, in 39-45 fms.; USS *Albatross* (Sta. 4233, N 55° W,

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Editor's Note: While it is our policy to use the metric system exclusively for all data pertaining to dimensions of specimens, weight, distances, volumes, and while we use the international abbreviations, we do, however, cite the "old" measurements and designations in items that are quoted from earlier literature, from labels or from correspondence. We consider the various data on depths in the present article as quotations and, therefore, have not converted them to the metric equivalents.

1 mi. from Cannery Point) coll., 8 July 1903. Holotype stated to be in the USNM, No. 214323.

Hypotypes (2). CASIZ Nos. 505a, 505b [SSB No. 27]. 2 measured specimens (1 ♂, 1 ♀) in an original series of 11 (4 ♂♂, 7 ♀♀) from 26-27 fms., Monterey Bay, California; USS *Albatross* (Sta. 4492, N 54° W, 7 mi. from Santa Cruz Lighthouse) coll., 18 May 1904.

Additional material see Table 1

Rossia pacifica diegensis Berry, 1912b: 292, 294.

Syntypes (2). CASIZ Nos. 457, 458 [SSB No. 19]. Type locality: 120-131 fms., off San Diego, California; USS *Albatross* (Sta. 4356, N 82°30′ E, 5.9 mi. from Point Loma Lighthouse) coll., 15 March 1904. The type lot (USNM 214376) stated to consist of 2 ♂♂ and 7 ♀♀, the primary types not designated by the author. Measurements of 1 ♂ and 1 ♀ are provided (p. 292) but the identity of these measured specimens is not indicated on the original labels.

Stoloteuthis [= *Sepiolina*] *nipponensis* Berry, 1911a: 39 to 41; 1 text fig.; 1912c: 414 - 417; plt. 5, figs. 1-4.

Holotype. CASIZ No. 459 [SSB No. 32]. Type locality: Suruga Bay, Japan; John O. Snyder, coll., 1900? A single ♂ for which measurements are provided (1912c: 416).

Naef (1912) has made this species the type of a new genus, *Sepiolina,* a step with which later teuthologists concur.

TEUTHOIDEA

Myopsida

Loliginidae

Loligo edulis Hoyle, 1885. Berry, 1912c: 398.

The Stanford Collection contained 3 lots of specimens that are now in the CASIZ Collection. These were collected in Japan in 1900 by David Starr Jordan and John O. Snyder; for details, see Table 1.

Loligo kobiensis Hoyle, 1885. Berry, 1912c: 398-399.

Stanford specimens now in the CASIZ Collection consist of 3 lots; for details, see Table 1.

Loligo opalescens Berry, 1911c: 591-592; 1912b: 294-297; plt. 43, figs. 5-8; plt. 44, figs. 2-4; plt. 45; plt. 46, figs. 4, 5.

Holotype. CASIZ No. 547 [SSB No. 101]. Type locality: Puget Sound, Washington. Type lot: 3 specimens taken by shrimp fishermen. Holotype, a ♂; "cotype" [= paratype], a ♀, deposited in the USNM, number not given; a second "cotype", a ♂, in the private collection of Dr. S. S. Berry, Redlands, California. Measurements of the primary types are provided (1912b: 296).

Hypotype. CASIZ No. 504 [SSB No. 65]. A measured immature specimen from 10 fms. (at anchor), off Pacific Beach, San Diego County, California; USS *Albatross* (Sta. 4324, N 24° E, 3.1 mi. from Point La Jolla) coll., 7 March 1904; one of a series of 6 specimens.

Additional material see Table 1

Loligo tetradynamia Ortmann, 1885. Berry, 1912c: 399 to 401.

Although no illustrated or measured specimens of this species were in the Stanford Collection, we are reporting on 4 lots in the CASIZ Collection from Japan (see Table 1).

Lolliguncula panamensis Berry, 1911b: 100-105; plt. 6; text figs. 1-7.

Holotype. CASIZ No. 537 [SSB No. 58]. Type locality: Panama, collected during the Hopkins-Stanford Expedition to the Galápagos Islands, 1898-99, by R. E. Snodgrass and Edmund Heller. Type lot: 3 ♀♀, the holotype being one of 2 indicated as "types" (p. 105) by the author, the other not found in the Stanford Collection, which, if extant, should be designated as a paratype.

Paratype. CASIZ No. 538 [SSB No. 58]. A ♀ designated by the author as a "cotype."

Another specimens [SSB No. 57] from Guyaquil, Ecuador, collected by P. O. Simons, is now in the CASIZ Collection.

Sepioteuthis arctipinnis Gould, 1852. Berry, 1914a: 308 to 310; plt. 54, fig. 1; text figs. 20-22.

Hypotype. CASIZ No. 573 [SSB No. 45]. A ♂, illustrated (*l. c.,* text figs. 21, 22) and measured (p. 310), from Honolulu, Oahu, Hawaii; D. S. Jordan and B. W. Evermann, coll., 1901.

Other Stanford specimens now in the CASIZ Collection include:

SSB No. 43. A juvenile from Honolulu Reef, Oahu, Hawaii, collected by Olaf P. Jenkins.

SSB No. 44. A ♀ from Honolulu, Hawaii, collected by Brandt.

Sepioteuthis lessoniana Lesson, 1830. Berry, 1912c: 401 to 404; plt. 6, figs. 3, 5.

Hypotype. CASIZ No. 574 [SSB No. 341]. A measured ♂ from Pusan, Korea, D. S. Jordan, coll., 1911.

Hypotype. CASIZ No. 534 [SSB No. 36]. A measured ♂ from Wakanoura, Kii, Japan; Jordan & Snyder, coll., 1900.

Additional material see Table 1

Oegopsida

Brachioteuthidae

Brachioteuthis (Tracheloteuthis) riisei (Steenstrup, 1882). Berry, 1914a: 336-338; text fig. 37.

Hypotypes (2). CASIZ Nos. 589, 590 [SSB No. 280]. 2 of an original series of 7 specimens taken at the surface S of Lanai and W of Kahoolawe, Hawaii; USS *Albatross* (Sta. 3878) coll., 14 April 1902. Berry (*op. cit.*: 337) provides measurements and illustrates one of them (fig. 37) but no information is available to indicate whether these particular specimens are correlated to the measurements or the illustration.

Cranchiidae

Liocranchia globulus Berry, 1909: 415-416; text fig. 9; 1914a: 346-348; plt. 53, figs. 2-4.

Paratype. CASIZ No. 520 [SSB No. 282]. Taken at the surface S of Lanai and W of Kahoolawe, Hawaii; USS *Albatross* (Sta. 3878, N 81°, E 51.2′ from Molokini Islet) coll., 14 April 1902. Indicated as "cotype," sex not specified. Holotype in the USNM, No. 214315 [SSB No. 262], the type lot consisting of 2 specimens.

Enoploteuthidae

Abraliopsis felis McGowan & Okutani, 1968: 72-79; plts. 9, 10; and distribution map.

Paratype. CASIZ No. 310. A ♂ from lat. 32°49′ N, long. 117°43′W, collected by the Scripps Institution of Oceanography, August 1953, during the California Cooperative Oceanic Fisheries Investigations sponsored by the Marine Research Committee of the State of California and the National Science Foundation. This specimen is designated by the authors as Paratype No. 2.

Abraliopsis felis appears to be a common species of the California Current with a range extending from the Oregon coast to Bahía Sebastion Vizcaino, Baja California, with a center of distribution off the vicinity of San Diego, California. It is said to be more abundant 80km or more offshore.

Abraliopsis scintillans Berry, 1911e: 93-94; 1912c: 425 to 432; plts. 7, 8, and 9, figs. 1-6; text figs. 3, 4.

Holotype. CASIZ No. 453 [SSB No. 147]. Type locality: Japan, probably off Misaki, Sagami. Type lot: 3 specimens, Alan Owston coll.?, indicated as "cotypes" numbered 1, 2, and 3 under SSB No. 147, all ♀ ♀ (1912c: 430). Presumably the specimen selected as the "type" [= holotype] and so labeled is SSB No. 147-1 with a mantle length of 59mm and a total length of 132mm.

Hypotype. CASIZ No. 507 [SSB No. 279]. A measured ♀ indicated as #6 in another series of 3 specimens under SSB No. 279, collected by Ishikawa at Misaki. The author states that one of the type lot (SSB No. 147-3) and one of the second series (SSB No. 279-5) were destroyed in dissection.

Later authors place this species in the genus *Watasenia* Ishikawa, 1913 (*e. g.*, Ishikawa, 1913; Sasaki, 1916: 94-95; and Okutani, 1967: 9), or treat *Watasenia* as a subgenus *of Abraliopsis* (McGowan & Okutani, 1968: 75).

Gonatidae

Gonatus [= *Berryteuthis*] *anonychus* Pearcy & Voss, 1963: 105-112; text figs. 1, 2; Stasek, 1966: 23.

Paratypes (2). CASIZ Nos. 23, 24. Collected under a night light about 80km off the coast of Oregon at the 1800m contour by the R/V *Acona* (Oregon State University) in lat. 42°49′30″N, long. 125°55′30″W, 10 July 1960. Specimens not sexed.

This species has been transferred to the genus *Berryteuthis* Naef, 1921, by Roper, Young & Voss (1969: 6).

Gonatus [= *Berryteuthis*] *magister* Berry, 1913a: 76-77; 1912b: 310-312; plt. 52, figs. 1, 2; plt. 53, figs. 1, 2; plt. 54, figs. 1-4; plt. 55, figs. 1, 3-7.

Holotype. CASIZ No. 463 [SSB No. 88]. Type locality: Puget Sound area, Washington, collected by shrimp fishermen, 1909. Type designated by Berry (1913a: 77), with measurements provided in an earlier report (1912b: 311) with accompanying illustrations (plt. 52, figs. 1, 2; plt. 53, fig. 1; plt. 54, figs. 1-3; plt. 55, figs. 1, 3, 4, 7).

Hypotype. CASIZ No. 525 [SSB No. 90]. A single specimen from near Victoria, British Columbia, Canada, taken from a salmon trap by J. B. Babcock, 1907. Measurements are provided for this specimen (Berry, 1912b: 311) as well as illustrations (1912b: plt. 53, fig. 2; plt. 54, fig. 4; plt. 55, figs. 5, 6).

Both of the above specimens were discussed originally under the name *Gonatus fabricii* (Lichtenstein, 1818). In establishing the new genus *Berryteuthis*, Naef (1921: 535) selected *Gonatus magister* Berry, 1913 as the type species (see also Young, 1972: 6).

Gonatus berryi Naef, 1923. Berry, 1912b: 308-312 (in part); plt. 52, fig. 3; plt. 55, fig. 2 (as *G. fabricii*); Naef, 1923: 245; Young, 1972: 46-49; table 2; plt. 15, fig. A; plt. 16, figs. A, C-I, L.

Berry (1912b: 311) listed several specimens of *Gonatus* with a range from near Victoria, British Columbia, Canada, south to the Coronados Islands, off upper Baja California, Mexico, under the name *G. fabricii* (Lichtenstein, 1818). Naef selected one of these [SSB No. 98] as the holotype of *G. berryi* on the basis of Berry's illustrations cited above. It is stated to be a juvenile trawled at a depth of 309-469 fms. in Monterey Bay, California, by the USS *Albatross* (Sta. 4512), 23 May 1904. As this specimen has not been found in the Stanford Collection, it is presumed to be in Dr. Berry's private collection in Redlands, California. Young (1972: 49) gives the known range of *G. berryi* as extending from latitudes 30° to 37° off southern California and Baja California.

Gonatus "fabricii (Lichtenstein, 1818)". Berry, 1912b: 308-312; plt. 52, figs. 1-4; plt. 53, figs. 1-6; plt. 54, figs. 1-4; plt. 55, figs. 1-7.

All of the specimens illustrated by Berry, as indicated above, now are considered to represent species of *Gonatus* other than *G. fabricii* [SSB Nos. 88, 90, 98, 100]. Of the remaining specimens listed [SSB Nos. 89, 95, 96, 97, 99] only Nos. 97 and 99 have been found in the Stanford Collection and are now in the CASIZ Collection, as follows:

SSB No. 97. A single juvenile from Monterey Bay, California, trawled in 755-958 fms. by the USS *Albatross* (Sta. 4530), 27 May 1904.

SSB No. 99. A single juvenile trawled in 581-594 fms. off San Nicolas Island, California, by the USS *Albatross* (Sta. 4424), 13 April 1904.

Both of these specimens may also belong to different species.

Gonatus onyx Young, 1972: 43-46; plt. 13, fig. A; plt. 14, figs. A, C-I; plt. 17, fig. J; Berry, 1912b: 308-312 (in part); plt. 52, fig. 4.

Young (1972: 43) states that Berry's illustration of a tentacular club, as indicated above, probably refers to *Gonatus onyx*. This particular specimen [SSB No. 100] was trawled in 724-1000 fms. in Monterey Bay, California, by the USS *Albatross* (Sta. 4544), 2 June 1904. It has not been located in the Stanford Collection and presumably has been deposited in Dr. Berry's private collection.

Ommastrephidae

Dosidicus gigas (d'Orbigny, 1835). Berry, 1911d: 304 to 306; plt. 20; plt. 21; text figs. 1-4; 1912b: 301-304; plt. 48, 49; text figs. 9-12 (illustrations copied from Berry, 1911d).

Hypotype. CASIZ No. 519 [SSB No. 72]. A large, measured and illustrated specimen from Monterey Bay, California, preserved whole, the sex not indicated. Total length 1.245 m (49 ins.); mantle length 63.5 cm (25 ins.). Formerly this giant squid specimen was in the collection of the University of California, Berkeley.

Sthenoteuthis [= *Ommastrephes*] *bartramii* (Le Sueur, 1821. Berry, 1912b: 298-300; plt. 47; plt. 50, figs. 4, 5; text figs. 7, 8.

Hypotype. CASIZ No. 535 [SSB No. 114]. A measured specimen Berry, 1912b: 300) illustrated as indicated above, blown on board a vessel off Komondorski Island, Bering Sea.

Another Stanford specimen of this species now in the CASIZ Collection is a single one from Sunday Island, Kermadec Islands, New Zealand, collected (probably) by W. R. B. Oliver of Auckland, 1908? [SSB number not assigned.]

For a discussion of the taxonomy of the Ommastrephidae see Voss (1963: 132-133).

Ommastrephes [= *Notodarus*] *hawaiiensis* Berry, 1914a: 338-341; plt. 54, fig. 2; text figs. 38, 39.

Hypotype. CASIZ No. 527 [SSB No. 244]. Trawled in 257-312 fms., vicinity of Kauai, Hawaii; USS *Albatross* (Sta. 4132, S 27°, W 27' off Hanamaulu warehouse) coll., 1 August 1902. A measured specimen (p. 340), sex not indicated.

Holotype in USNM No. 214382 [SSB No. 243]. In his report on the R/V *Endeavor* cephalopods, Berry (1918) considered his species should be transferred to the genus *Notodarus* Pfeffer, 1912, along with *Ommastrephes sloani* Gray, 1849, from New Zealand.

Todarodes pacificus Steenstrup, 1880. Berry, 1912c: 433 to 437; plt. 6, fig. 4 (right third arm); as *Ommastrephes sloani* Gray, 1849

Hypotype. CASIZ No. 575 [SSB No. 256]. A measured specimen (p. 435, numbered "286" in error) from Tokyo, Japan; Jordan & Snyder, coll., 1900.

Hypotype. CASIZ No. 576 [SSB No. 257] Five

measured specimens in a series of a total of 9 from Hakodate, Oshima, Japan; Jordan & Snyder, coll., 1900.

Hypotype. CASIZ No. 577 [SSB No. 258]. One measured specimen from a lot of 2 from Hakodate, Oshima, Japan; Jordan & Snyder, coll., 1900.

Hypotype. CASIZ No. 578 [SSB No. 273]. A single measured specimen from Tomakomai, Iburi, Japan; John O. Snyder, coll., 1900.

Another specimen from the Stanford Collection now in the CASIZ Collection is SSB No. 259, collected by Jordan and Snyder at Misaki, Sagami, Japan, in 1900.

Okutani (1967: 12) places this species in the family Todarodidae, raising this taxon from the subfamily level (Voss, 1963: 128).

Rhyncoteuthion [= *Ommastrephes*] [alpha] Berry, 1914a: 341-343; plt. 53, fig. 1.

Hypotype. CASIZ No. 518 [SSB No. 255]. Taken at the surface, eastern Pacific Ocean between the Hawaiian Islands and Laysan Island in lat. 21°13′ N, long. 158°43′W; USS *Albatross* (Sta. 3926) coll., 10 May 1902. One of 5 specimens in the lot, measured (p. 342) and illustrated as cited above.

It now has been determined that all species in the genus *Ommastrephes* d'Orbigny, 1835, pass through a 'rhyncoteuthis' larval stage, recognized by a fusion of the tentacular arms to form a trunk-like proboscis. This is indicated by Berry in his discussion of the above form (see Roper, Young & Voss, 1968: 10).

Rhyncoteuthion [= *Ommastrephes*] [beta] Berry, 1914a: 343.

A single specimen [SSB No. 246], taken at the surface between Oahu and Laysan Islands, Hawaii, by the USS *Albatross* (St. 3930, lat. 25°07′N; long. 170°50′W) 15 May 1902, has not been found in the Stanford Collection.

Onychoteuthidae

Moroteuthis robusta (Verrill, 1876). Berry, 1912: 314 to 315.

There were no specimens of this species in the Stanford Collection. Smith (1966) listed a total of 13 records for specimens collected off the west coast of North America in the period 1872 to 1962, 4 of which (numbers 8 and 11 to 13 in the list) are in the CASIZ Collection. Two of these are adults over 2.7 m in total length, preserved whole in formalin. Other occurrences of *Moroteuthis robusta* off the coast of California and Oregon have been reported by Van Hyning & Magill (1964), Pearcy (1965: 261 to 262) and Philipps (1966). Young (1972: 38) says no specimens of this large squid were taken with a 3 m Isaacs Kidd mid-water trawl in any of the 445 mid-water tows made by the R/V *Velero* IV in the period 1960 to 1966 off southern California and Guadalupe Island, Mexico. Most of the offshore captures have been made by commercial trawlers operating at depths of 150 m or more.

The beaks of *Moroteuthis robusta* are illustrated by Iverson & Pinkas (1971: fig. 38) as are those of most of the species of cephalopods occurring in California waters.

Onychoteuthis banksii (Leach, 1817). Berry, 1914a: 322-323; text fig. 31.

Hypotype. CASIZ No. 526 [SSB No. 227]. A measured specimen from the vicinity of Laysan Island (pp. 86-87), illustrated as cited above; Max Schlimmer, coll.

Onychoteuthis borealijaponica Okada, 1927. Berry, 1912a: 83-87; text figs. 44-46; 1913a: 77 [as *O. banksii* (Leach, 1817)]. Young, 1972: 61-64; plt. 18, fig. A; plt. 19, figs. A-G.

Hypotype. CASIZ No. 542 [SSB No. 295]. A ♀, measured (Berry, 1912a: 86-87) and illustrated (*ibid.*, figs. 44-46), taken with a seine off the entrance to Newport Bay, California, by J. H. Souder.

OCTOPODA

Cirromorpha

Opisthoteuthidae

Opisthoteuthis californiana Berry, 1949: 23-26; 1952: 183-188; text figs. 1-5.

Holotype. CASIZ No. 548 [SSB No. 858]. A ♀ trawled in 188 fms. NW x W off Eureka Bar, Humboldt County, California; M/V *Andrew Jackson* (Capt. N. Franklin) coll., 25 April 1948.

A paratype (partially dissected ♀) is indicated as deposited in Dr. Berry's private collection [SSB No. 859]. Subsequently, Berry (1955) described and illustrated a ♂ trawled in 280 fms. off Humboldt County, California. According to Phillips (1966), collecting records for *Opisthoteuthis californiana* range from Monterey to Eureka, California, in depths of 344-580 m (188-317 fms.). The frequency and number of specimens collected appears to be in a direct ratio to the number of deep-water hauls made by commercial otter trawlers. The CASIZ Collection contains other specimens of this deep-water octopod.

Incirrata

Octopodidae

Polypus [= *Octopus*] *apollyon* Berry, 1912b: 280-284; plt. 35, fig. 3; plt. 36, fig. 1; plt. 39, fig. 4. Covered under the name *Polypus hongkongensis* (Hoyle, 1885).

Paratype. CASIZ No. 461 [SSB No. 145]. A measured ♂ from Uyak Bay, Kodiak Island, Alaska, taken in the course of a U. S. Fish Commission Salmon Investigation; USS *Albatross* coll. at one of a series of stations numbered 4287 to 4290, inclusive, 14 August 1903. This specimen, indicated on original labels as a "cotype," is designated herein as a paratype as it was collected with the holotype.

The holotype of *Polypus apollyon* was designated by Berry (1912b: 284, footnote a) and deposited in the U. S. National Museum of Natural History (USNM No. 214 319). According to Pickford (1964: 28), it no longer can be found and is presumed lost. Thus, it is fortunate that a second specimen from the type lot collected in Uyak Bay, Alaska, has been located in the Stanford Collection even though it, too, was thought to be lost. Should the loss of the holotype be confirmed, the above designated paratype becomes available for selection as a lectotype of Berry's species. See discussion under the species designation *Polypus hongkongensis,* below. According to Pickford (1964: 51-52), the cold-water race of the Pacific giant octopus occurring in Bering Sea, Kamchatka, Okhotsk Sea, the Kurile Islands, and Alaska, should take the name *Octopus dofleini apollyon* (Berry, 1912).

Polypus [= *Octopus*] *areolatus* de Haan, 1838. Berry, 1912c: 393-396; text fig. 1.

Hypotype. CASIZ No. 503 [SSB No. 148]. A measured ♂ (Berry, 1912c: 395) fromTsuruga, Echizen, Japan, Jordan & Snyder, coll., 1900.

Additional material see Table 1

Polypus [= *Octopus*] cf. *P. areolatus* de Haan, 1838. Berry, 1912c: 395-396

Hypotype. CASIZ No. 509 [SSB No. 332]. A single large measured ♂ (Berry, 1912c: 396) collected at Tsuruga, Echizen, Japan, by Jordan & Snyder, in 1900 is designated as a hypotype herein because of the author's statement that it "is not only much larger than any other specimens above referred to *P. areolatus* but differs from them so conspicuously in several quite important characters that I feel considerable uncertainty as to whether it is specifically identical with them."

Polypus [= *Octopus*] *bimaculatus* (Verrill, 1883). Berry, 1912b: 278-280; plt. 34; plt. 35, fig. 2; plt. 39, fig. 5.

Hypotype. CASIZ No. 528 [SSB No. 123]. A measured ♂ (Berry, 1912b: 279) from San Diego, California; Edwin C. Starks, coll.

Hypotype. CASIZ No. 529 [SSB No. 103]. A measured ♀ from off La Jolla, California; William E. Ritter & William J. Raymond, coll. (San Diego Marine Biological Association), 1901. Beak dissected out of this specimen and illustrated (Berry, 1912b: plt. 39, fig. 5), but not preserved with the remainder of the specimen.

Hypotype. CASIZ No. 543 [SSB No. 324]. Berry 1912a: 87; text figs. 47, 48. A single specimen, sex not indicated, from Laguna Beach, Orange County, California, C. F. Baker (from original label) coll., 25 June 1911.

Syntypes of this species are said to be in the USNM (Robson, 1929: 79). Regarding other Stanford specimens, see Table 1.

No attempt has been made here to distinguish between *Octopus bimaculatus* and its sibling species *O. bimaculoides* Pickford & McConnaughey, 1949 (the so-called "mud-flat octopus" of southern California), this being left to the judgment of a specialist. According to these authors, CASIZ Hypotypes No. 528 and 529 [SSB Nos. 123 and 103] probably are *O. bimaculatus.*

Polypus [= *Octopus*] *californicus* Berry: 1911c: 590; 1912b: 286-288; plt. 35, figs. 6, 7; plt. 38; plt. 39, figs. 1, 2; plt. 40, figs. 2, 3; text fig. 3.

Paratype. CASIZ No. 460 [SSB No. 131]. Type locality: 191-192 fms., off La Jolla, San Diego County, California; USS *Albatross* (Sta. 4325, SE of Point La Jolla, off Soledad Hill, 4.4 mi) coll., 8 March 1904. A measured ♂ (Berry, 1911c: 287). The type lot consists of 3 ♂ ♂, the holotype designated as a "type" by the author and deposited in the USNM (No. 214321). Berry does not indicate which of the 3 measured animals is the "type." The other 2 animals (indicated as "cotypes") are designated as paratypes herein, one of which is the above specimen. The remaining paratype presumably is in the private collection of Dr. Berry, Redlands, California.

Hypotypes (2). CASIZ Nos. 530, 531 [SSB No. 135]. Two measured ♂ ♂ from off San Diego, California, trawled in 193-227 fms.; USS *Albatross* (Sta. 4323, off Point Ja Jolla, 3.7 mi. SE of Soledad Hill) coll., 7 March, 1904.

Hypotype. CASIZ No. 532 [SSB No. 135]. A meas-

ured ♀ from 260-284 fms., off San Diego; USS *Albatross* (Sta. 4369, S 82° E, 10 mi. from Point Loma Lighthouse) coll., 16 March 1904.

Additional Stanford specimens now in the CASIZ Collection include 3 juveniles out of the original series of 4 [SSB No. 126] trawled in 130-158 fms. off San Diego; USS *Albatross* (Sta. 4365) coll., 16 March 1904.

Polypus [= *Octopus*] *fontanianus* d'Orbigny, 1835. Berry, 1914a: 299.

The Stanford Collection contained a fairly large ♀ [SSB No. 355] collected in the Bay of Callao, Perú, by Admiral Beardsley. This is now in the CASIZ Collection.

Polypus [= *Octopus*] *gilbertianus* Berry, 1912b: 284-286; plt. 35, figs. 4, 5; plt. 36, fig. 2; plt. 37.

Paratype. CASIZ No. 510 [SSB No. 140]. A measured ♂ (Berry, 1912b: 285), indicated as "cotype" by the author, is designated herein as a paratype. It comes from 188-131 fms. in Stephens Passage, Alaska; USS *Albatross* (Sta. 4253, vicinity of the Stikine River delta, N 53° E, 1.7 mi. from Thistle Ledge) coll., 14 July 1903. This specimen, thought to be lost by Pickford (1964: 32), fortunately was found in the Stanford Collection.

The holotype (indicated as a "type" by the author) was deposited in the USNM, No. 214320 [SSB No. 139]. Type locality: 41-134 fms., vicinity of Naha Bay, Behm Canal, southeast Alaska; USS *Albatross* (Sta. 4228) coll., 7 July 1903.

After a careful study of Berry's holotype and other available data, Pickford (1964: 32-33; 36-38, 49) concludes that *Octopus gilbertianus* should be considered a synonym of *O. dofleini apollyon* (Berry, 1912).

Polypus [= *Octopus*] *hongkongensis* (Hoyle, 1885). Berry, 1912b: 280-284; text fig. 2.

Specimens described and listed under this species name by Dr. Berry, which were preserved in the Stanford Collection and now are in the CASIZ Collection are listed in Table 1, below.

Because all of the specimens listed under this name in Table 1 were identified initially as *Polypus hongkongensis*, and also because none of them was collected at the type locality of *Octopus apollyon* in Uyak Bay, Alaska, none of them can be designated objectively as hypotype even though Berry provides measurements for some of them. Furthermore, another species of *Octopus, O. rubescens* Berry, 1953, with a range at least as far north as Monterey Bay, must be taken in consideration.

For a discussion of the relationship between *Octopus hongkongensis* and *O. apollyon* see Robson (1929: 199 to 204) and especially Pickford (1964: 25-26, 28-30) for a commentary on the particular specimens reported upon by Berry, collected in the Pacific Northwest and off the coast of California. Robson assigns both species to the genus *Paroctopus* Naef, 1923 (syn. *Pseudoctopus* Grimpe, 1925), which is a genus no longer considered valid (Pickford & McConnaughey, 1949: 57).

As a result of the detailed and painstaking analysis of data and other evidence relating to the giant octopus of the North Pacific, Pickford concludes that there are 3 distinguishable races, as follows:

Octopus dofleini dofleini (Wülker, 1910)

From the western Pacific (Japan and Korea)

Octopus dofleini apollyon (Berry, 1912)

From subarctic regions of the northern Pacific (Bering Sea, Kamchatka, Okhotsk Sea, Kurile Islands, and Alaska)

Octopus dofleini martini Pickford, 1964

From temperate eastern Pacific (Washington, ?California)

Presumably, the giant octopus occurring on the coast of Oregon and central California (and possibly farther south) should be identified as *Octopus dofleini martini*, at least provisionally until a comprehensive analytical study of populations inhabiting this extensive stretch of coastline can be made. In view of the misunderstanding resulting from identifications of the Pacific giant octopus as *O. hongkongensis*, great credit is due Dr. Pickford for her authoritative determination that this is a Japanese species distinct from *O. dofleini*. It should be noted here also that she relegates *Polypus gilbertianus* Berry, 1912 to the synonymy of *O. dofleini apollyon* (Berry, 1912).

Polypus [= *Octopus*] *hoylei* Berry, 1919: 407-408; text fig. 1; 1914a: 296-298; plt. 47, fig. 1; plt. 48, figs. 2-4; plt. 55, fig. 1; text fig. 15.

Hypotype. CASIZ No. 462 [SSB No. 176]. A measured ♂ (Berry, 1914a: 298) from 283-309 fms. off Kauai, Hawaii; USS *Albatross* (Sta. 4130, N 61°; W 2.2′ from Hanamaulu warehouse) coll., 1 August 1902.

The holotype (indicated as "type" by the author) deposited in the USNM, No. 214310 [SSB No. 166]. Type locality: Hawaiian Islands; the specific locality is unknown because of the loss of the original locality label.

Polypus [= *Octopus*] *leioderma* Berry, 1911c: 590-591; 1912b: 288-289; plt. 35, fig. 1; plt. 40, figs. 4, 5.

The Stanford Collection contained no type specimens of this species. Holotype, a ♀ in the USNM, No. 214322 [SSB No. 137]. Type locality: 106-112 fms. in Shelikov Strait, Alaska; USS *Albatross* (Sta. 4293) coll., 15 August

1903. Another specimen in the Stanford Collection and now in the CASIZ Collection, listed by BERRY (1912b: 289) [SSB No. 173], was trawled in 110-170 fms. in the Gulf of Georgia, British Columbia, Canada; USS *Albatross* (Sta. 4194) coll., 20 June 1903. It is a female.

Polypus [= *Octopus*] *macropus* (Risso, 1826). BERRY, 1912c: 389-390.

Hypotype. CASIZ No. 579 [SSB No. 325]. A measured ♂ (BERRY, 1912c: 390) from Aomori, Mutsu, Japan; Jordan & Snyder, coll., 1900.

Hypotype. CASIZ No. 580 [SSB No. 327]. A measured ♂ from an original series of 3 specimens (1 ♂, 2 ♀ ♀) from Matsushima, Rikuzen, Japan; Jordan & Snyder, coll., 1900.

Additional material see Table 1 .

Polypus [= *Octopus*] *marmoratus* (Hoyle, 1885). BERRY, 1914a: 291-293; plt. 45; plt. 48, fig. 6; text fig. 13.

Hypotype. CASIZ No. 539 [SSB No. 174]. A measured ♂ (BERRY, 1914a: 292) from the Honolulu fishmarket, Oahu, Hawaii; collected in 1889 (or 1901); illustrated in BERRY, *op. cit.*, plt. 45 (whole animal) and on plt. 48, fig. 6 (hectocotylized portion of third right arm).

Hypotype. CASIZ No. 533 [SSB No. 175]. A measured ♂ from Honolulu, Jordan & Evermann, coll., 1901. BERRY, 1914a, text figure 13 shows the funnel organ.

Another Stanford specimen, now in the CASIZ Collection, is a juvenile from Henshaw's Road, Hilo, Hawaii [SSB No. 181].

According to ROBSON (1929: 94-98) *Octopus marmoratus* is conspecific with *O. cyaneus* Gray, 1849, and should be considered as a synonym of this latter species. Syntypes of *O. cyaneus* are stated to be in the British Museum (Natural History), London.

Polypus [= *Octopus*] *oliveri* Berry, 1914b: 136-137; plt. 6, fig. 2.

Paratype. CASIZ No. 464 [SSB No. 405]. A measured ♀ (BERRY, 1914b: 137) designated as a "cotype" by the author, was collected with the holotype off Sunday Island, Kermadec Islands, New Zealand, by W. R. B. Oliver in 1908.

The holotype, designated as "type" by the author, has a total length of 175 mm, the paratype, somewhat larger, being 190 mm, but less well preserved. ROBSON (1929: 100) states the holotype possibly may be deposited in the Dominion Museum, Wellington, New Zealand.

Polypus [=*Octopus*] *ornatus* (Gould, 1852). BERRY, 1914 b: 294-296; plt. 46, text fig. 14.

Hypotype. CASIZ No. 506 [SSB No. 179]. The smaller of 2 measured ♂ ♂ (BERRY, 1914b: 295) has a total length of 263 mm, is from Honolulu reef, Oahu, Hawaii; USS *Albatross* (Sta. no. not indicated), coll., 1902.

Another Stanford specimen now in the CASIZ Collection is a juvenile, also from Honolulu Reef, collected by O. P. Jenkins, 1889 [SSB No. 186].

Polypus [= *Octopus*] *pricei* Berry, 1911d: 303-304 (as *Polypus* sp., young); 1913a: 73-75; text fig. 2 (inner aspect of right ventral arm).

Holotype. CASIZ No. 454 [SSB No. 189]. A measured specimen (BERRY, 1913a: 74), sex not specified, from off Point Pinos, Monterey Bay, California, in the stomach of a salmon; C. H. Gilbert, coll. 23 June 1911. One of 4 specimens.

Paratypes (2). CASIZ Nos. 455, 456 [SSB No. 189]. Part of the type lot.

BERRY (1913a) states the type lot is composed of a "type" and "cotypes," herein designated as holotype and paratypes, respectively. Measurements for one of the paratypes are provided but there is no published or label information that indicates to which one of the 3 specimens these apply. The third paratype has not turned up in the Stanford Collection and presumably is deposited in the Berry Collection, Redlands, California.

Octopus rubescens Berry 1953. BERRY, 1912b: 281-284; plt. 39, fig. 3 (as *Polypus hongkongensis*); 1953: 51-52.

Hypotype. CASIZ No. 568 [SSB No. 134]. A measured ♂ (one of 2 specimens, the other an unmeasured ♀) trawled in 75-134 fms. off San Diego, California; USS *Albatross* (Sta. 4349, NE 6.5 mi. from Point Loma Lighthouse) coll., 12 March 1904. This specimen was included with others in Berry's discussion of *Polypus hongkongensis*, but was assigned later by him to *Octopus rubescens* (BERRY 1953: 52).

Type locality of *Octopus rubescens*: 7-17 fms. off the east and south shores of South Coronado Island, Baja California, Mexico; Carl L. Hubbs, J. W. Sefton, *et al.*, collectors, on the R/V *E. W. Scripps* and the R/V *Orca*, 1948-1949. Holotype [SSB No. 969] and 18 paratypes [SSB Nos. 968, 970, 972, 976] in the Berry Collection.

In discussing the published measurements of several of Berry's California specimens, initially identified as *Polypus hongkongensis*, PICKFORD (1964: 25) concluded that 2 specimen-lots, collected by Harold Heath at Pacific Grove, Monterey Bay, California, might be assigned to *Octopus rubescens*. These are SSB No. 146, 1 ♂ and other of indeterminate sex; and SSB No. 153, 1 ♂ and 2 ♀ ♀. They are now in the CASIZ Collection. In addi-

tion, she considered a ♂ [SSB No. 81] from 15-18 fms., off the Coronado Islands, Baja California, Mexico, collected by Ritter and Raymond (San Diego Marine Biological Association, Sta. LVIII, Haul 1, 1901), might be identified as *O. rubescens* also. This particular specimen, however, was not found in the Stanford Collection.

Polypus [= *Octopus*] *vulgaris* (Cuvier, 1797). Berry, 1912c: 386-388.

Hypotype. CASIZ No. 540 [SSB No. 337]. A measured ♂ (Berry, 1912c: 387) from Fusan [=Pusan], Korea; D. S. Jordan, coll., 1911; one of 2 specimens, both ♂ ♂. As this measured animal is 355 mm in total length to tip of arms (mantle length, dorsal, 71 mm), the other having a total length of 610 mm, it seems probable it is the one herein designated as a hypotype.

Hypotype. CASIZ No. 541 [SSB No. 339]. A measured ♂ from Tsuruga, Echizen, Japan; Jordan & Snyder, coll., 1900.

Additional material see Table 1

Polypus [= *Octopus*] α (young) Berry, 1909: 418 (listed only); 1914a: 299-300; text fig. 16.

Hypotype. CASIZ No. 523 [SSB No. 192]. A meassured juvenile (Berry, 1914a: 299) taken with a night-light off the south coast of Molokai, Hawaii; USS *Albatross* (Sta. 3843, N 68°45′ W, 2.8 mi. from Lae-o Ka Laau Lighthouse) coll., 4 April 1902. One of 2 specimens collected.

Berry (1914a: 300) believes this form may be the young of *Octopus ornatus* Gould, 1852.

Polypus [= *Octopus*] β (young) Berry, 1909: 418 (listed only); 1914a: 300-301; plt. 48, figs. 7, 8.

Hypotype. CASIZ No. 584 [SSB No. 195]. An illustrated specimen (1 of 2 juveniles, Berry, 1914a: plt. 48, fig. 8) taken at the surface off the south coast of Oahu, Hawaii; USS *Albatross* (Sta. 3921) coll., 6 May 1902.

Other Stanford specimens now in the CASIZ Collection include: SSB No. 184, a small animal from shore on Honolulu Reef, Oahu, Hawaii; and SSB No. 201, another small specimen taken at the surface off Diamond Head, Oahu, Hawaii, by USS *Albatross* (Sta. 3907), 5 May 1902.

Polypus [= *Octopus*] γ (young) Berry, 1909: 418 (listed only); 1914a: 301-303; text figs. 17, 18.

Hypotype. CASIZ No. 521 [SSB No. 180]. A measured ♀ (Berry, 1914a: 302), illustrated as cited above, taken from shore at Honolulu, Oahu, Hawaii; Dr. Wood, coll., 1898.

Hypotype. CASIZ No. 522 [SSB No. 188]. A measured ♂ from Honolulu Reef, O. P. Jenkins, coll., 1889.

Berry says this form is not the young of *Octopus ornatus* Gould, 1852, nor of *O. hoylei* (Berry, 1909), and differs in a number of characters from *O. marmoratus* Hoyle, 1885.

Polypus [= *Octopus*] δ (young) Berry, 1914a: 303.

A single, badly mutilated juvenile specimen taken on the reef at Honolulu by Dr. Olaf P. Jenkins is stated to be in the Stanford Collection, but has not been found. It is SSB No. 186, which Dr. Berry says "recalls *P. ornatus* but in most ways the aspect is notably different."

Polypus sp. Young. Berry, 1912c: 391-392.

SSB No. 344, now in the CASIZ Collection, includes 4 small specimens, 3 of them measured, collected by Snyder and Sindo at Taneshima Island, Japan. All are stated to be males. Dr. Berry provides the following comments: "These specimens in certain ways suggest the *P. globosus* of Appelöf, but the order of the arms is decidedly different, and the hectocotylus, though very much smaller, is of a similar type to that prevailing in the *hongkongensis* group. The possibility has not been overlooked that they may be young *P. dofleini,* but here again the arm formulae fail to coincide."

Scaeurgus patagiatus Berry, 1913b: 564; 1914a: 305-307; plt. 47, figs. 2, 3; plt. 48, fig. 1; text fig. 19.

Hypotype. CASIZ No. 501 [SSB No. 207]. A measured ♀ (Berry, 1914a: 306) from 132-141 fms., Pailolo Channel between Maui and Molokai, Hawaii; USS *Albatross* (Sta. 4103, N 32°45′ E, 6.7 mi. from Mokuhooniki Islet) coll., 23 July, 1902. One of a lot of 3 specimens (1 ♂, 2 ♀ ♀), all measured.

Hypotype. CASIZ No. 502 [SSB No. 206]. A measured ♂ from 128-138 fms. in the Pailolo Channel; USS *Albatross* (Sta. 3858, N 35° E, 8.1 mi. off Mokuhooniki Islet) coll., 9 April 1902.

The holotype, a male, is stated to be in the USNM, No. 214379 [SSB No. 204]. Type locality: In 143-178 fms. off Puniawa Point, Maui, Hawaii; USS *Albatross* (Sta. 4079) coll., 21 July 1902.

Ocythoidae

Ocythoe tuberculata Rafinesque, 1814. Berry, 1916b: 1-4; 1 text fig.; 1955: 177-181; text fig. 2.

Hypotype. CASIZ No. 536 [SSB No. 453]. A large, measured ♀ (total length 440; body length, 160 mm), illustrated as cited, from near Avalon, Santa

Catalina Island, California; collected by W. E. Hamilton, summer of 1915.

For more recent records of this species, see Young (1972: 92-93).

Tremoctopodidae

Tremoctopus violaceus delle Chiaje, 1829. Berry, 1914a: 281-286; plt. 49, figs. 3, 4; text figs. 8-10.

Hypotypes (2). CASIZ No. 581, 582 [SSB No. 218]. 1 ♂ and 1 ♀, both measured (Berry, 1914a: 285) from an original lot of 5 specimens (2 ♂ ♂, 3 ♀ ♀) taken at the surface off Molokini Islet, Kahoolawe, Hawaii; USS *Albatross* (Sta. 3878) coll., 14 April 1902.

Hypotype. CASIZ No. 583 [SSB No. 221]. A single measured ♀ from an original lot of 3 specimens (1 ♂, 2 ♀ ♀) taken at the surface between Oahu, Hawaii, and Laysan Island in lat. 25°07′, long. 170°50′W; USS *Albatross* (Sta. 3930) coll., 15 May 1902. As measurements are provided for both females in the lot, the one designated as a hypotype must be selected on the basis of agreement with the specimen having a total length of 64+mm, or the other having a total length of 51+mm. Also, one of these females is illustrated (Berry, 1914a: text figs. 8, 9), but which is not specified on original labels.

Another specimen of this species now in the CASIZ Collection is a male [SSB No. 220] also taken at the surface between Oahu and Laysan Island by the USS *Albatross* (Sta. 3829, lat. 23°19′N, long. 166°54′W), 13 May 1902.

Table 1

Sepia kobiensis (Hoyle, 1885)			
349 [1]	Nagasaki	Jordan & Snyder, 1900	10 [2]
350	Off Honshu	USS *Albatross* (Sta. 3741), 1906	1
351	Off Honshu	USS *Albatross* (Sta. 3713), 1906	5
352	Off Honshu	USS *Albatross* (Sta. 3708), 1906	3
353	Off Honshu	USS *Albatross* (Sta. 3714), 1906	1
354	Hakodate Bay	USS *Albatross* (Sta. 3657), 1906	1
357 [1]	Hakodate	Jordan & Snyder, 1900	1
358	Off Hokkaido	USS *Albatross* (Sta. 3729), 1906	1
359 [1]	Hakodate	Jordan & Snyder, 1900	3 [3]
362	Off Hokkaido	USS *Albatross* (Sta. ?), 1906	1
378	Off Honshu	USS *Albatross* (Sta. ?), 1906	1
Euprymna scolopes Berry, 1913			
296	Shore at Honolulu		2 juveniles
297	Shore at Honolulu		1 male, 1 female
299	Shore at Honolulu		4 males, 5 females
306	52 - 56 fms. off Maui		1 female
307	Surface, off Molokai		2 juveniles
315	127 - 128 fms. off Molokai		1 female
Rossia pacifica Berry, 1911			
55	Puget Sound, Washington		12 (males & females)
24	Off mouth of Salinas River, Monterey Bay, California		3 [4]
2	20 - 30 fms., Monterey Bay, California		2 females
Loligo edulis Hoyle, 1885			
372	Bay of Waka, Kii		2 males
373	Aomori, Mutsu		30+ juveniles
374	Aomori, Mutsu		4 juveniles

Loligo kobiensis Hoyle, 1885

365	Onomichi, Bingo, Japan	1 male, 1 female
366	Nagasaki, Hizen, Japan	2 females
396	Osaka, Japan	1 female

Loligo opalescens Berry, 1911

59	Off Pacific Grove, California	3 males, 3 females
66	San Diego, California	2 juveniles
67	San Diego, California	2 juveniles
68	20 - 30 fms., off mouth of Salinas River, Monterey Bay, California	3 juveniles
69	Monterey Bay, California	3[5]
107	Deception Pass, Washington	1 male

Loligo tetradynamia Ortmann, 1885

369	Same, Mutsu	2 males
370	Tokyo	6 males, 8 females
371	Kawatana, Hizen	1 male, 1 female, 5 juveniles
393	Okayama, Hizen	1 male

Sepioteuthis lessoniana Lesson, 1830

35	Tsuruga, Echizen, Japan	1 female
37	Misaki, Sagami, Japan	2 juveniles[6]
38	Nagasaki, Hizen, Japan	4 juveniles
40	Misaki, Sagami, Japan	9 juveniles
41	Bay of Waka, Kii, Japan	4 juveniles
342	Pusan, Korea	5 of both sexes[7]
39	Apia, Samoa	3 specimens

Polypus areolatus de Haan, 1838

329	Aomori, Mutsu	2 males
330	Bay of Waka, Kii, Japan	1 female
347	Tokyo, Japan	1 male
348	Tokyo fishmarket	1 juvenile

Polypus bimaculatus (Verrill, 1883)

102	Off La Jolla, San Diego County, California	2 females
104	Off La Jolla, San Diego County, California	1 female
121	San Diego, California	3 (2 juveniles)
122	San Diego, California	1 (not sexed)
124	San Diego, California	4 juveniles
Not assigned	Mazatlán, Sinaloa, Mexico	1 (not sexed)

Polypus hongkongensis (Hoyle, 1885)

154	Karluk, Kodiak Island, Alaska	3 juv. female
144[8]	Port Townsend, Washington	1 juv. female
149	Port Townsend, Washington	1 juv. female
162[8]	Port Townsend, Washington	2 males, 1 female
214	Crescent City, Del Norte County, California	1 juvenile
151[8]	Point Reyes, Marin County, California	1 male
143[8]	Monterey Bay, California	1 female, 2 juveniles
150	Monterey Bay, California	1 juv. female
155	Monterey Bay, California	1 juv. female
158[8]	Monterey Bay, California	1 male

159	Monterey Bay, California	1 juv. female
160	Monterey Bay, California	4 juv. females
164 [8]	Monterey Bay, California	4 juveniles
87	Off San Diego, California	2 juveniles
152	Off San Diego, California	1 female
Polypus macropus (Risso, 1826)		
326	Bay of Waka, Kii, Japan	1 female
328	Hakodate, Oshima, Japan	1 male
346	Misaki, Sagami, Japan	1 female
Polypus vulgaris (Cuvier, 1797)		
334	Pusan, Korea	1 female
336	Misaki, Sagami, Japan	1 male
338	Tsuruga, Echizen, Japan	3 females
345	Misaki, Sagami, Japan	1 female

[1] listed, BERRY, 1912c: 423; [2] of an original series of 13
[3] of an original lot of 4; [4] of an original lot of 7 (2 ♂♂, 5 ♀♀)
[5] of an original lot of 24; [6] of an original lot of 3
[7] of an original lot of 6; [8] measured specimens

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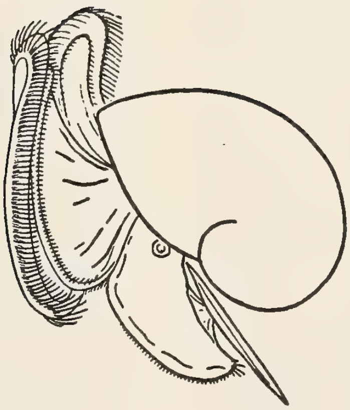

NOTES & NEWS

Miscellaneous Observations on *Rumina decollata* (Linnaeus, 1758) (Achatinidae) and a Request

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Because of its spotty distribution and known history of certain of the infestation sites, *Rumina decollata* (Linnaeus, 1758) is assumed to have been in California at least from the mid-1950s. It was first reported from that state in 1966 (Fisher, 1966).

A listing compiled by T. Kono, California State Department of Food and Agriculture in February and May, 1973 (personal correspondence) reports *Rumina decollata* from a total of 17 sites in the counties of Imperial, Kern, Los Angeles, Orange, Riverside, San Bernardino, San Diego, and Ventura.

In California *Rumina decollata* is classified as a "B" pest which means it is rather widely distributed and occurs in localized populations, but eradication is not considered to be feasible, nor necessary.

The author has made random observations on scattered populations in Riverside, San Bernardino, and Los Angeles counties and has seen no direct evidence that *Rumina decollata* feeds on growing plant material. It was further observed that if *R. decollata* is present, *Cryptomphalus (Helix) aspersa* (Müller, 1776) is either absent in the immediate area or is present in much smaller numbers than is *Rumina*. County agricultural inspectors and others who have reported infestations of *R. decollata,* have upon being questioned confirmed similar observations in retrospect. A few such people have made confirming follow-up observations.

In California, *Rumina decollata* seems to occur only where water has been supplied by man, *i.e.*, in situations where the natural habitat has been disturbed for horticultural or agricultural activities. In areas of the United States with higher rainfall it would be of interest to learn if *R. decollata* has become established "in the wild" and what its influence has been on mollusks native to those areas, or to exotic species which have become likewise established.

In the laboratory in December 1972 and January and February 1973 tests utilizing aquaria of 18 and 36 l capacity containing 5 cm of soil have repeatedly demonstrated that *Rumina decollata* overtly attacks and devours *Cryptomphalus aspersa* as well as the limited number of worm and slug species which were offered as food. Cannibalism is also suspected, but the state of health of the victims at the time of attack is unknown. One guess is that if they had been feeling robust, they would have been diners, not dinners. Further tests in the aquaria concerned only certain plant materials offered as food, and *Rumina* performed in accord with its omnivorous reputation, but with some selectivity expressed. When given a choice of raw and slightly cooked slices of carrots and beets, and leaves of lettuce, chard, and beets, it consumed them in the order given. When given a choice of whole or cut (halved) avocado and orange fruits, *Rumina* nibbled first at the cut fruit. Whole oranges, when placed directly on the soil or when elevated from direct contact with the soil by shallow petri dishes, and in the absence of other edibles, were nipped in characteristic snail fashion. However, when half the surface of the soil was covered with a 2½ cm layer of damp decaying leaves taken from a citrus grove, no feeding occurred on fruit placed on the humus or soil during 3 days. Because these tests were conducted at room temperature, and the snails were active, it is assumed that they sought the habitat afforded by the decaying leaves and fed on the organic material thus provided in preference to the fruit which only the day before they had fed on in the absence of humus. Approximately 40 snails were utilized per test and many eggs were deposited in the soil against the glass bottoms of the aquaria. Contents of the several eggs which were examined were watery, and it is suspected that they were infertile.

Another test in a 36 l capacity aquarium involved half ponies of young plants of Marigold (Yellow First Lady), Pepper (Jalapeno), Petunia (Maytime, F_1 hybrid), and Tomato (Pearson improved). These plants were set in soil to a normal planting depth and surrounded by about 2½ cm of decaying citrus leaves. At the end of 48 hours the Marigolds, Petunia, and Pepper were reduced to shredded stumps, but the tomato leaves were only cursorily nibbled. Although such intensive feeding occurs under confined conditions in the laboratory, nothing to match it or even come close to it has been observed by the author in nature. At one of the original discovery sites in Riverside, a home garden which consists of a mixed planting of several species of herbaceous ornamental plants and vegetables, and from which over 600 viable *Rumina decollata*

were easily collected during one visit in 1973, no snail damage is obvious.

The foregoing observations raise certain questions regarding the true pest status of *Rumina decollata,* and more importantly suggest the possibility that this species might be used for the biological control of *Cryptomphalus aspersa,* which is a serious pest throughout most of California, and for which home gardeners as well as many agriculturists spend more for poison baits than they do for all other pesticides combined. Controlled field tests are in the planning stages to critically examine the interactions of *Cryptomphalus-Rumina* populations. Certain of the tests will be conducted at the University of California, Riverside, and others will be in cooperation with Mr. Wendell Young, Deputy Agricultural Commissioner, San Bernardino County.

In case an earlier hint passed unnoticed, the author hereby presumptuously requests correspondence from persons who have access to populations of *Rumina decollata,* and who can take time and effort to observe by actual count its abundance and range of sizes (*i.e.,* less than 1 cm and more than 1 cm) relative to the numbers and species of terrestrial mollusks present in the top 4 cm of soil in one or more approximated square meters per site. Locality data and a brief description of the habitat should be included in the report. Notes on observed feeding habits would be of special interest. Correspondents will be properly acknowledged should the solicited information be incorporated into a future publication.

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Range Extension for *Dendronotus diversicolor*

(Mollusca : Opisthobranchia)

BY

GORDON A. ROBILLIARD

Woodward-Envicon, Inc.

3489 Kurtz Street, San Diego, California 92110

In the original description, the geographic range of *Dendronotus diversicolor* Robilliard, 1970, included the Ogden Point Breakwater in Victoria, British Columbia, and several locations in the San Juan Islands, Washington. This range was based on animals I collected between September 1966 and May 1968. More intensive collecting from May 1968 to May 1971 indicated that *D. diversicolor* was seasonally abundant at numerous other locations in these same general areas (Robilliard, 1971). In the same period, the range was extended about 96 km west to the exposed west coast of Washington when I found a single specimen at 26 m on Spike Rock (Long. 124°43′24″ W; Lat. 48°15′N), September 8, 1969. This 35 mm long animal, white with orange tips on the cerata, and veil and crown papillae, was eating a thecate hydroid, *Abietinaria amphora* Nutting, 1904. On August 9, 1971, I collected 5 specimens ranging from 20 to 25 mm in length at 11 m near Schooner Cove on the west coast of Vancouver Island (Long. 125°48′30″ W; Lat. 49°03′ N), a range extension of 176 km northwest of the San Juan Islands. The color combinations were: white ground color with orange tips on cerata and other appendages (3 animals); purple ground color with orange tips on cerata, etc. (1 animal); and white ground color with opaque white tips (1 animal). All 5 were eating the thecate hydroid *A. traski* (Torrey, 1902) and at least one specimen had deposited several egg masses on the hydroid.

That *Dendronotus diversicolor* was present in California, specifically central California from Bodega Bay to Monterey Bay was inferred from the description by Marcus (1961) under *D. frondosus* (Ascanius, 1774). In his description, Marcus included animals which were "... white with orange-yellow points on the principal branches of the appendages." (p. 34). In my experience, *D. frondosus* does not exhibit this color pattern, but it is a common one for *D. diversicolor* (Robilliard, 1970; 1971; unpublished observations). Confirmation of the presence of *D. diversicolor* as far south as Pismo Beach, California, came from Steven J. Long, Richard R. Roller, and Allyn G. Smith who sent me slides or descriptions of specimens, or both. These data represented an increase in range of approximately 1600 km south from the type locality.

Finally, on May 10, 1973, I obtained a small (12 mm long) *Dendronotus diversicolor* at 17 m in the Point Loma kelp bed about 6½ km north of Point Loma, San Diego, California (Long. 117°14′30″ W; Lat. 32°39′55″ N). This animal was white with orange tips on the cerata and veil and crown papillae, and was eating an unidentified species (probably *Abietinaria* sp.) of thecate hydroid. I have observed other specimens in the San Diego-Oceanside region of California on several occasions between January 1972 and May 1973, but have not recorded specific data. These observations extend the known range of

D. diversicolor about 440 km south from Pismo Beach and a total of about 2040 km south from the type locality.

ACKNOWLEDGMENTS

I would like to acknowledge Gerry Likens for typing the manuscript and Woodward-Envicon, Inc. for financial support. The master of the RV *Squeg*, Captain Alan D. Grant is acknowledged for his assistance in diving operations. My wife, Helen, assisted as diving partner and in preparing the paper.

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Ethnomalacology and Archaeomolluscan Studies in North Mexico, Mesoamerica, and Central America

BY

LAWRENCE H. FELDMAN

Over the past half century many archaeological, or anthropological, reports discussing non-European use of mollusks have appeared. For Mexico and Central America the literature is particularly rich. Because of their publication in journals and books remote from the view of most malacozoologists, it was felt that a summary of the more important articles of recent years would be of value to many.

The Reference Bibliography is divided into 4 sections: Areal Studies; Religious and Ceremonial Usage Articles; Functional Usage Articles; and Paleo-Ecological Papers. Areal studies provide species lists and summaries of all pertinent literature from a limited geographical area. Their bibliographies should be consulted by those seeking additional citations for the cultural use of shells in a particular area. Other papers, including an areal study of Central Mexican shells and a discussion of West Mexican ceramic shells are in preparation. The author hopes eventually also to prepare a monograph discussing all aspects of prehispanic Mexican and Central American employment of mollusks. Paleo-ecological papers provide more detailed information on natural range, natural habitat or intraspecies variation for the time periods between the end of the Pleistocene and the 16th century A. D. than is generally found in most archeological reports. In this way they provide a valuable link between the investigations of paleontologists and those who study the living mollusks.

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ERRATUM

In the paper by Dr. Alan Solem, "A New Genus and Two New Species of Land Snails from the Lau Archipelago of Fiji (Mollusca : Pulmonata : Endodontidae)" published in The Veliger 16 (1): 20 - 30, figures *1* to *4* were numbered incorrectly. The numbers should be changed as follows:

no. *2* should be no. *1*,
no. *4* should be no. *2*,
no. *1* should be no. 3,
and no *3* should be no. *4*.

Generous Donations Received

The Conchological Club of Southern California added a very generous amount of money to our Endowment Fund. This was a repetition of an equally generous gesture of about a year earlier. We express our appreciation for this continued support from our friends.

The Southwestern Malacological Society of Phoenix, Arizona, sent a generous donation to the Veliger Endowment Fund. This gift, like those received from other sources, will continue to assist us in keeping the cost of our journal at a lower level than would otherwise be possible. We interpret such donations as signs of confidence in, and approval of our efforts and we are very grateful.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of $5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is $25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

Important Notices

It is with great regret that we must announce the following increases in Membership Dues and Subscription Rates. effective with volume 16:
Membership Dues are US$12.00; to this we must add US$1.50 for members living in Canada, Mexico, Brazil, and all Spanish speaking countries (postally known as PUAS-countries); for members in all other foreign countries, the postage charge will be US$2.00. The basic subscription rate is set at US$25.00; to this must be added the same postage charges as for members.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US$6.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US$12.00 for all foreign addresses (including PUAS).

Because of the peculiar rate-fixing policies of the Postal Service (the so-called "temporary rates" which may be put in effect without advance notice, pending a final decision by the Rate Fixing Commission) we must reserve the right to ask our members and subscribers for additional payment for postage charges; however, because of the rather high cost such an extra collection would cause, we expect to absorb any but unbearable increases. That such increased charges may have to be reflected in future price schedules is evident.

REGARDING POSTAL SERVICE

It is general knowledge that in spite of the optimistic statements made in the propaganda disseminated by the U. S. Postal Service, the service continues to deteriorate. Regrettably, however, the United States of America is not alone in this respect. Evidence is accumulating in our offices to the effect that irregularities occur in other countries as well; to our surprise, Japan is one of these. Since we have designed a system which makes it impossible to omit mailing copies of our journal to any member or subscriber who is paid up, and because of the regulations pertaining to the second class mailing permits, we know that if a copy does not reach the addressee, the fault lies with the postal system of the country or area of destination. Our complaints to the local Post Office can bear no fruit in such cases. We must request our members and subscribers to inquire at their local post offices if their copies do not arrive. We cannot replace lost copies free of charge and, unless the journal were mailed by insured post, the Post Office will not indemnify the injured party. The losses we have sustained in the past years have been mounting steadily, and not in proportion to our increased circulation.

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address). We are not able to replace lost copies free of charge but must charge single copy rates. There will, of course, be only the usual charge of $1.00 for re-forwarding a copy *IF* it has been returned by the post office to us. We also must urge our members and subscribers to place written complaints with the U. S. Post Office Department in case of loss, as every copy of our journal carries our guarantee for return postage. Thus, destruction of a copy of our journal by postal employees constitutes gross negligence and the person concerned deserves an official reprimand, at least.

We must call the attention of our Members and Subscribers to the fact that we mail our journal on the date stated on the cover of a particular issue. After we have delivered the journal to the Post Office, our control ends. Delays in delivery seem to become more and more common. Needless to say that we regret this very much; we had hoped that when the salaries of the Postal Workers were increased, the service would improve. However, this seems not to be the case.

Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

Requests to be placed on this special mailing list should be sent to the Manager, Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$2.50 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.00 face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Moving?

If your address is changed it will be important to notify us of the new address at least **six weeks** before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

change of address – \$1.-

change of address and re-mailing of a returned issue – \$2.-.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

By mutual consent, our contract with Kraus Reprint Co. to reprint our out-of-print volumes has been cancelled. However, we are investigating other possibilities and will announce any conclusion we may reach eventually.

California Malacozoological Society, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

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Publication Date of THE VELIGER

The publication date of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Post Office does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

BOOKS, PERIODICALS, PAMPHLETS

Intertidal Mollusks of Iquique, Chile

by LOUIE MARINCOVICH, Jr. Los Angeles County Natural History Museum Science Bulletin 16, 49 pp.; 102 figs. [of mollusks], 20 February 1973.

This is a well illustrated account of the relatively unstudied intertidal mollusks of northern Chile. Ten of the 88 species from Iquique (lat. 20° S) are described as new; a columbellid genus, *Salitra,* is also new. Most of the mollusks are restricted to the Peruvian Molluscan Province (lat. 6 to 42° S). Ranges for these species are plotted in a table showing adjacent equatorial and eastern South Pacific molluscan provinces. Some ranges are revised based upon the author's study of unpublished material in museum collections. Included is an overview of the Peruvian Molluscan Province and problems concerned with recognition of its boundaries. There are detailed data on the intertidal distribution and substrate preference of each species.

WOA

The Aquatic and Land Mollusca of Texas
Part two: The Recent and Pleistocene members of the Pupillidae and Urocoptidae (Gastropoda) in Texas

by E. P. CHEATUM & R. W. FULLINGTON. Dallas Museum of Natural History Bulletin no. 1. 67 pp.; 7 plts.; 13 maps. $4.50. 1973

This second part carries on the tradition of excellence established with the first part. Regrettably, the senior author died on May 1, 1973, and thus could not see the finished work. However, the junior author, a close coworker of Dr. Cheatum, promises to carry on the work. In a letter, Dr. Fullington indicates that the suddenness of the death poses a number of problems; for example, there appear to be no records of unfinished correspondence or of borrowed or loaned material and Dr. Fullington is very anxious to carry on the work. He may be contacted at the Dallas Museum of Natural History, P. O. Box 26193, Fairpark Station, Dallas, TX 75226.

RS

How to Clean Seashells

by EUGENE BERGERON. 32 pp.; illust. Great Outdoors Publishing Co., 4747 28th Street North, St. Petersburg, Florida 33714; $1.-.

This small pamphlet contains hints on cleaning shells, but it also gives advice on shipping shells safely as well as on labeling and displaying a collection. The pamphlet may be helpful to beginners.

RS

A Field Guide to Shells of the Atlantic and Gulf Coasts and the West Indies

by PERCY A. MORRIS, edited by W. J. CLENCH. 3rd edition, Houghton Mifflin Co. $7.95; paperback $4.95., 1973.

More than a generation of shell collectors have used earlier editions of this guide, and a fair percentage were first "hooked" on shells through its influence. In providing illustrations of over 500 species, it long proved to be a handy and useful manual. Unfortunately, descriptions were less than precise, there were many errors in names and the nomenclature remained uncorrected in later editions, and no references where the reader could seek further reading or information were listed. These defects seriously limited its value in years past.

The lifetime learning of Bill Clench is everywhere in evidence for what is really a new book. Not only are all the plates redone and greatly improved, but the species coverage has doubled and been expanded geographically to include part of the West Indies. The descriptions have been tightened and revised to a model of clarity, the introduction significantly expanded, a list of references for further reading added, and the glossary enlarged.

This book is now highly recommended for all collectors of marine shells. Dr. Clench and the publishers are to be congratulated on producing such a highly useful and fine book. The only unfortunate feature is the fabrication of "common names" for each species, with the scientific names relegated to second place and in smaller type. While the latter may strike the novice as tongue twisters, at least the name can be followed from book to book. Until an authentic list of common names appears, however, each author is free to make up his own and does so!

Alan Solem

Card Catalogue of World-Wide Shells.

Pack # 1 – Marginellidae

by SALLY DIANA KAICHER. ii+98 cards. For sale by the author, 5633B 18th Way South, St. Petersburg, Florida 33712. $3.-; 1973

Each 3 x 5 inch card in this series contains name and authorship of a marginellid species, front and back views (with magnification specified) of a representative speci-

men, a short descriptive notation, and the general geographic area in which the species is found. Species are assigned to genera in accordance with modern concepts of marginellid systematics. Of particular interest is the figuring, for the first time, of several species described by DALL (1927, Proc. U. S. Nat. Mus. **70:** 1 - 134) with photographs of type lot material from the USNM. The advantages of the card file format are obvious. The disadvantages stem mainly from the brevity which the small format imposes; but the backs of the cards are free for annotations. *Persicula phrygia* (Sowerby), actually widespread in the Panamic province, is cited only as "Galapagos." Other card packs, covering other families, are planned.

B. Roth

Freshwater Snails of Taiwan (Formosa)

by GARY L. PACE. Malacological Review, Supplement 1: 118 pages; 19 plates; 17 text figures; 2 tables. 1973. (received November 10, 1973)

This is an important work as it is concerned with 39 species of freshwater snails from Formosa. Not only are classification, distribution, and zoogeographic affinities considered, but the parasitological importance of the various species is discussed, an importance lying in the fact that several of the species are intermediate hosts for some of the dread parasitic diseases affecting man and other homoiothermal animals. Thus, this work is of importance not only for malacologists but also for parasitologists and public health workers.

RS

SOOSIANA

Number 1, volume 1 of what appears to be a new malacological journal, named in honor of the Hungarian malacologist Lajos Soós, has just reached our desk.

As far as we are able to ascertain, this will be an annual publication. It is produced by photo-offset printing from typewritten copy. The articles are written in Hungarian, some having a brief abstract in German, others in English, and one or two have no abstract at all. Line drawings are used liberally. Unusual to most readers will be the fact that slashes (/) are used instead of parentheses. However, nomenclature used seems to be modern and precise, including authorship and year of original description.

Unfortunately no indication of the availability of this new journal is evident. However, we are convinced that more details may be obtained by writing to Dr. A. Richnovszky, Dósza str. 12-14, Baja, Hungary. We would have done so ourselves but we wished to bring this new publication to the attention of those of our readers who are interested in the molluscan fauna of Hungary at the earliest possible moment.

RS

Kelp Habitat Improvement Project Annual Report: 1 July 1971 - 30 June 1972

WHEELER J. NORTH, Principal Investigator. W. M. Keck Laboratory of Environmental Health Engineering, California Institute of Technology. 200 pp., illust. 1973.

This is the ninth report of an on-going project. As in previous years, the book includes specialized reports prepared by various investigators. It becomes evident that the problem of "reforestation" of the once almost completely denuded kelp beds is a very complex one and it is also evident that this problem is approached from as many different angles as possible. New problems are not unexpectedly arising each year - or, rather - are discovered each year. Healthy, productive kelp beds are of great importance in many ways to the human population and perhaps from the narrow point of view of the malacologist very important as potential food and shelter for many species of mollusks.

RS

Additional Type Specimens of Fossil Invertebrata in the Collections of the Natural History Museum of Los Angeles County

by GALE G. SPHON. Contributions in Science No. 250, Los Angeles County Natural History Museum, 75 pp. July 5, 1973.

Approximately 11 pages of this pamphlet are devoted to molluscan types of one sort or another. The section on literature would be more valuable if the copy had been proof-read by a person with a thorough knowledge of German typography; as it is, the peculiar so-called "long-s" has been misread for an f throughout. Other errors have crept in through misreading of other German letters of what in German typography is called "Fraktur", a type face apparently too different for the person with only a limited knowledge of the language. However, the list in itself is not affected by these shortcomings and is to be considered a desirable contribution.

RS

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

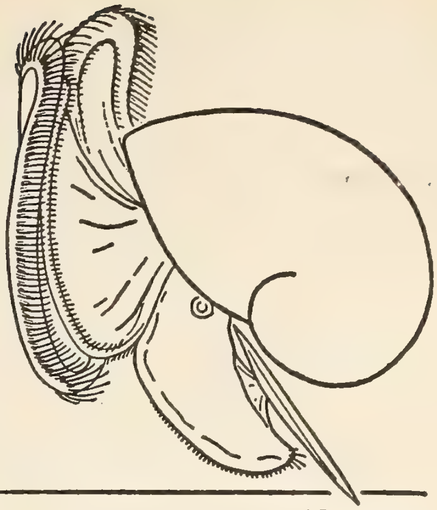
Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

THE VELIGER



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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, **DIVISION**, **Subdivision**, **SECTION**,
SUPERFAMILY, FAMILY, Subfamily, *Genus,* *(Subgenus)*
New Taxa

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Four New Species of Nudibranchs from Tropical West America

BY

HANS BERTSCH [1] AND ANTONIO J. FERREIRA [2]

(7 Plates)

SINCE 1969 WE HAVE MADE numerous research trips to the tropical West American faunal province. Some of the new information we have found appeared earlier in this journal (e.g. BERTSCH *et al.*, 1973). In this paper, we describe three new species we have collected from the northern Panamic province, and one new species from the Galápagos Islands collected by Gale G. Sphon.

CHROMODORIDIDAE Bergh, 1891

Thorunna Bergh, 1878

Thorunna ***lapislazuli*** Bertsch and Ferreira, spec. nov.

(Figures *1* and *5* to *9*)

Material examined: Four specimens collected intertidally at the Charles Darwin Research Station, Academy Bay, Galápagos Islands (0° 45′ S; 90° 15′ W), in March, 1971, by Gale G. Sphon.

1) **Holotype:** Intact whole animal, deposited in the collections of the California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type Series no. 595.

2) **Paratypes:** One dissected radula (Figures *5* to *9*), mounted on a microscope slide, deposited in the collections of the California Academy of Sciences, CASIZ Type no. 596 (CASIZ Type Slide Series, no. 367).

3) Two specimens deposited as additional paratypes at the Los Angeles County Museum of Natural History, LACM no. 1614.

[1] Donner Laboratory, Lawrence Berkeley Laboratory, and (mailing address) Department of Zoology, University of California, Berkeley, California 94720; Associate, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118

[2] Beta Research Oceanographic Laboratories, Inc., 2060 Clarmar Way, San Jose, California 95128

Description: Lengths of preserved specimens vary from 4 to 6 mm. Body is the typical chromodorid shape, with mantle margin extending over the sides of the animal's body.

Coloration consists of light blue, navy blue, and orange yellow (Figure *1*). An irregular dorsal median stripe of light blue begins anterior to the rhinophores, widens just behind the rhinophores and then becomes thinner, continuing back to just before the gills. A large area of dark navy blue completely encloses the mid-dorsal light blue stripe, with a patch of navy blue extending across the notum at about ½ the animal's length. This navy blue region is randomly covered with dots and splotches of orange and light blue. The mantle is edged completely by a light blue band. The tail protrudes out behind the posterior portion of the mantle, and has a navy blue streak down its center, which is dotted with orange patches; a light blue band occurs on the border of the foot. The six simply pinnate gills (held upright and close together) and the perfoliate rhinophores are navy blue, with whitish tips.

Radular formula 41 (46–50·1·0·1·46–50). The rows were counted down the center; at the extreme posterior end (lower right hand corner of Figure *5*), the last 3 or 4 rows were not continuous nor easily counted because of the damaged condition of that part of the radula. The half-row formula was based on counts of teeth in the right half of rows 15 through 18. No rachidian tooth. First lateral tooth (Figures *6* and *7*) with a base 2–3 times as broad as the following lateral teeth; rectangular base, which splits at about ½ its length into a thin prong on the inner side, and a bi- and tricuspid upright, backward-curving hook on the outer portion of the tooth; with 2 or 3 smaller denticles on the posterior surface of the outer hook. The rest of the lateral teeth bicuspid, with a narrow base. Some of the inner laterals are strongly hook-shaped (Figure *8*), with 1 to 3 denticles on the posterior surface; the upper bicuspid tip at times bent over the lower tip of the same tooth. Outer laterals are more erect, with only the bicuspid tips forming a pronounced hook (Figure *9*); there are up to 5 denticles on the posterior surface of the cusp. The upright shaft is not straight, but bends con-

vexly on the outer surface from where it arises at the base to the tip of the cusp. This curvature allows the teeth in the same row to overlap slightly with each other, providing a stronger cutting edge across the entire radular row. This pattern of articulation between teeth of the same row is accompanied by an inter-row overlap and interdigitation between the elongate bases of the teeth. Such a double interlocking system can be compared with teeth articulation patterns in two other Panamic chromodorids. *Hypselodoris agassizii* (Bergh, 1894) exhibits a similar double interlocking (Ferreira and Bertsch, in prep.), but the upright shafts of the teeth are much shorter, and the bases sturdier than in *Thorunna* ***lapislazuli***. On the other hand, *Chromodoris marislae* Bertsch, 1973, has only the overlap and interdigitation between the bases of different rows of teeth (Bertsch *et al.*, 1973).

Discussion: The generic placement of this species, and its relationship with other genera of Chromodorididae, need explanation.

The two most common genera of Chromodorididae are distinguished by their body shapes and radulae. *Hypselodoris* Stimpson, 1855, has a body approximately quadrilateral in sectional shape, without an ample pallial skirt (Thompson, 1972); the radula lacks a median tooth and the lateral teeth are deeply bicuspid. *Chromodoris* Alder and Hancock, 1855, usually has a widely projecting mantle skirt, and the radula has unicuspid lateral teeth. The distinction is not always clear, because of overlapping characteristics.

Kay & Young (1969) describe the radula of the Hawaiian *Hypselodoris vibrata* (Pease, 1860) as having unicuspid outer teeth, and bicuspid inner teeth. However, their illustration does not show the characteristic bicuspid shape; moreover, scanning electron micrographs (by Bertsch) of the radula of a specimen collected in Hawaii by Terrence M. Gosliner (December 1972) reveal that all the teeth are unicuspid. The animal is also characterized by a broad, overhanging mantle edge. It should be classified (under the current understanding) as *Chromodoris vibrata*.

Roller (1970) placed the eastern Pacific *Chromodoris porterae* Cockerell, 1902, in the genus *Hypselodoris*, without any explanatory statements. The description by MacFarland (1966) describes the radular teeth as "apparently bifid at the tip." However, an examination of the radula and the drawings by MacFarland (1966:plt. 34) reveals that the teeth are not bicuspid—they do not have the two large cusps obviously differentiated in size from the denticles occurring in a row along the upright cusp. This species, also, belongs in the genus *Chromodoris*.

The new species, *Thorunna* ***lapislazuli***, has an obvious *Chromodoris*-type body form. However, the lateral teeth have the bicuspid shape typical of *Hypselodoris*. The generic placement of our new species, then, required an obvious differentiating characteristic. In searching the literature, we found two Indo-Pacific genera distinguished by a unique innermost lateral tooth: the relatively unknown *Thorunna* Bergh, 1878, and *Noumea* Risbec, 1928. Neither of these genera had previously been reported from the eastern Pacific, although *Thorunna picta* (Pease, 1860), new combination, occurs in Hawaii (cf. Kay and Young, 1969, for its synonymy), and the Panamic *Chromodoris tura* Marcus and Marcus, 1967, has a radula which places it among the *Thorunna-Noumea* group (= *Thorunna tura*, new combination).

Thorunna was established by Bergh to accommodate the Philippine species *furtiva*. He described the genus (Bergh, 1878: 575) as having a chromodorid body shape, with no labial armature, rachis naked, and innermost lateral tooth much broader than the following lateral teeth. Bergh later emphasized (1892: 119) that *Thorunna* is almost completely similar to *Chromodoris*. Eliot (1908: 110) reported *T. furtiva* from the Red Sea, and Marcus & Marcus (1960: 901–902) reported two specimens of *Thorunna* sp. from the Maldive Islands in the northern Indian Ocean. The only other reports of this genus that we could find in the literature were discussions on its taxonomic placement. Thiele (1931: 433) placed it in the subfamily Thorunninae; Odhner (1939: 26) changed it to the Acanthocyclinae, quoted by Marcus & Marcus (1967: 167) as Actinocyclinae. Most recently, Odhner (in Franc, 1968) classified *Thorunna* in the Chromodorididae, and placed *Noumea* as a synonym of the older species. He gave no reasons for the synonymy, but did give a generic description, with no mention at all of labial armature.

The genus *Noumea* was named by Risbec (1928) to include three species from New Caledonia. Since then, additional species of *Noumea* have been named by Risbec (1930), Baba (1937; 1949), Burn (1966), and Marcus &

Explanation of Figures *1, 2*

Figure *1*: *Thorunna* ***lapislazuli*** Bertsch & Ferreira, spec. nov.; photograph by David K. Mulliner

Figure *2*: *Laila janssi* Bertsch & Ferreira, spec. nov.; photograph by Antonio J. Ferreira of a Costa Rican specimen

Figure *1*

Figure *2*

Marcus (1970 a). The genus includes those species of chromodorids with a radular formula of n.1.0.1.n., the first lateral tooth with a highly enlarged base (Risbec, 1928: 165). Baba (1949: 144) states that *Noumea* differs from *Glossodoris* only in that the 1^{st} lateral tooth is differentiated from the following laterals by being decidedly broader, and Marcus & Marcus (*op. cit.*: 163) characterize *Noumea* as chromodorids with the innermost lateral tooth twice as broad as the following ones.

Apparently, the only difference between *Noumea* and *Thorunna* is that *Thorunna* lacks labial armature. The decision to synonymize these genera must rest on an evaluation of the generic significance of the presence or absence of labial armature among the chromodorids. Marcus & Marcus (1970 a: 163) have judged that the "radulae furnish the best generic characters. The jaw elements, rods, hooks, or platelets, are useful for the separation of the species." Based on an extension of this opinion to include labial armature as being only of specific importance, we have followed Odhner's synonymy of the genera, and have named our Galapagan new species, *Thorunna* ***lapislazuli.***

Thorunna ***lapislazuli*** differs in its coloration and radular pattern from the known species of *Thorunna.* None of the others have the inner spike on the 1^{st} lateral tooth. Of the Panamic chromodorid species, *T.* ***lapislazuli*** is most similar to *T. tura.* The notum of *T. tura* has a dark violet center, with scattered fire-red spots, and *T.* ***lapislazuli*** has a light blue center, with orange spots in the navy blue area around the periphery of the center. *Thorunna* ***lapislazuli*** has a larger number of teeth per row than *T. tura,* and has an inner spike on the 1^{st} lateral tooth which *T. tura* lacks.

The name ***lapislazuli*** was chosen in reference to the blue coloration of this animal.

Polyceratidae Alder & Hancock, 1855
(emended spelling, Keen, 1971)

Laila MacFarland, 1905

Laila ***janssi*** Bertsch and Ferreira, spec. nov.

(Figures *2* and *10* to *15*)

Material examined: 1) **Holotype:** One specimen collected subtidally (in 5–7 meters of water under a rock on a sandy bottom) in Bahía Santa Elena, Guanacaste, Costa Rica (10° 56′ N; 85° 49′ W), on February 13, 1972, by Antonio J. Ferreira. The intact whole animal has been deposited as the holotype in the collections of the California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type no. 597.

2) **Paratype:** Dissected radula (Figures *10* to *15*), mounted on a microscope slide, of a second specimen collected at Bahía Santa Elena (under the same rock with the holotype) by Antonio J. Ferreira on February 13, 1972; deposited in the collections of California Academy of Sciences, CASIZ Type no. 598 (CASIZ Type Slide Series no. 368).

3) **Additional records:** Nine specimens, in 1 foot of water, on the west side of Isla Partida (24° 33′ N; 110° 24′ W) in the southern Gulf of California, on August 12, 1973, by Antonio J. Ferreira. Largest specimens measured 8 mm in body length.

Laila janssi has a range of over 2000 km, from the southern Gulf of California to northern Costa Rica.

Description: Oval body shape, fringed with rows of bulbous pallial processes; dorsal surface raised slightly along the central portion (Figure *2*). Body length of preserved holotype 3.4 mm; width, 2.0 mm; larger pallial processes 1.7, 2.6, and 2.4 mm long. Dorsum smooth, except for a row of about 9 papillae, the same yellow orange color as the dorsum surface, situated lengthwise along the center of the notum, beginning anterior to the rhinophores and ending in front of the gills. Body color yellow-orange, with numerous small orange dots covering the dorsum and foot. About three irregular rows of numerous orange, club-shaped papillae completely surround the notum, projecting from the pallial margin; papillae increase progressively in size from the outer ones inward. Largest papillae (about 9–10 per side), almost ⅓ the body length of the animal, exhibit an exaggerated club-shape, with the distal ½ to ⅔ of its length greatly inflated. Smaller lateral processes (more than 18 per side) are less markedly club-shaped. Papillae anterior to rhinophores are thin and elongate, only slightly spindle-shaped; about ¼ of them are almost twice as long as the other frontal papillae. All papillae are yellow-orange colored; the specimens from Costa Rica had a prominent apical white dot, whereas the specimens from Isla Partida had a small dark orange dot. This was the only difference between the populations that we found.

Rhinophores are orange, with about 10–13 leaves on the clavus.

The 3 long, tripinnate orange gills are in a triangular grouping, one anterior and one on each side of the anal opening.

Length of radula is three times its width. Radula formula of paratype is 59 (8–14·1·1·0·1·1·8–14); the last three rows are poorly differentiated. Rachis consists of a row of single, nearly square plates (Figures *10* and *13*), with two parallel ridges running lengthwise along the center of the plates. The innermost of the two pleural teeth in each half-row is a thin, straight shaft, the distal third ending in a posteriorly-directed hook (Figure *14*). The base of the tooth is widened into a lateral flange on the outer side; this flange articulates into the curved inner surface at the base of the second pleural tooth. This hook is completely worn away in the first 16 anterior rows. The outer pleural tooth is a thick, branching structure (Figures *10, 14* and *15*). About ⅓ the distance from its base, the outer surface curves laterally to a wing-like point, then curves inward until the shaft bifurcates at the top. The distal end of the shaft is formed into two hooks, an inner, small one pointing posteriorly, and a large lateral hook which protrudes at right angles to the inner cusp and main shaft, and then curves sharply downwards bent back against the side of the shaft (Figures *14* and *15*). The outer laterals are closely set, approximately quadrangular in shape (Figures *11* and *12*). The posterior surface is evenly concave. The inner edge of the posterior surface forms a sharp point. Along the inner edge of the entire tooth, a ridge increases in height from the sharp posterior point to the raised anterior flange. Below this ridge is a groove which articulates with the outer side of the adjacent inner tooth (Figure *12*). The anterior edge of the tooth is fairly straight, except for a slight depression just before the raised anterior flange.

Discussion: There is only one other species of the genus known, *Laila cockerelli* MacFarland, 1905, which occurs along the Pacific coast of the United States and in the northern part of the Panamic province (Lance, 1961). *Laila cockerelli* has two morphological variations: a northern form, ranging from Vancouver Island, British Columbia, Canada, to Point Conception, California, which has low white tubercles scattered randomly over the notum; and a southern form, ranging from Point Conception south along the Pacific coast to Cabo San Lucas, Baja California, Mexico, and then north in the Gulf of California to Bahía de los Angeles, Baja California, which has a single row of red tubercles spaced irregularly down the center of the notum (Keen, 1971).

Laila cockerelli and *L. janssi* are closely related; the general radula pattern and body shapes are similar, but striking differences exist which readily permit a specific separation. The body color of *L. cockerelli* is pure white, while that of *L. janssi* is light yellow, with numerous small orange dots covering the dorsum; the pallial processes of *L. cockerelli* are white, tipped with red-orange, whereas *L. janssi* has light orange processes with an apical white dot. *Laila janssi* has a row of papillae down the center of the notum, separating it from the northern form, with the color of the papillae the same as the rest of the dorsum, separating it from the southern form of *L. cockerelli*. *Laila cockerelli* has 5 branchial plumes; *L. janssi* has only 3.

The radula of *Laila cockerelli* has been described by MacFarland (1906: 135; 1966: 105) and Marcus (1961: 21–22), and differs in at least four ways from that of *L. janssi:* 1) the number of teeth rows is apparently less in *L. janssi;* 2) the rachidian plate of *L. janssi* has a rough texture with parallel ridges, whereas it is smooth in *L. cockerelli;* 3) the large outer cusp on the 2nd pleural tooth of *L. janssi* is much longer and curls back down along the length of the shaft, but it is short and protrudes fairly straight off the main shaft in *L. cockerelli;* 4) the shape of the outer lateral teeth of *L. janssi* have a deeper indentation on the posterior surface, and the anterior inner flange occurs on all the lateral teeth, but in *L. cockerelli* this flange is developed only in the first four lateral teeth, and then becomes obliterated in the outer teeth.

The specific name *janssi* was chosen to honor Mr. Edwin Janss, Jr., artist-photographer and collector of nudibranchs, in appreciation for his contributions to malacozoology and his support and encouragement of researchers in the field.

Explanation of Figures *3, 4*

Figure *3*: ***Flabellina stohleri*** Bertsch & Ferreira, spec. nov.; photograph by Hans Bertsch

Figure *4*: ***Phidiana lascrucensis*** Bertsch & Ferreira, spec. nov.; photograph by Antonio J. Ferreira of a specimen collected March 21, 1971, in Bahía Banderas, Nayarit, Mexico

Figure 3

Figure 4

Flabellinidae Bergh, 1890

Flabellina Voight, 1834

Flabellina ***stohleri*** Bertsch and Ferreira, spec. nov.

(Figures *3* and *16* to *21*)

Material examined: Seven specimens collected subtidally in 2 to 3 meters of water at the lower end of the bay south of Punta San Francisquito (28° 26′ N; 112° 52′ W), Baja California, Mexico, on August 24, 1971, by Hans Bertsch, Eugene V. Coan, and Ray Holiday. The animals were found, in the mid-afternoon, crawling among algae that was on top of rocks. This diurnal behavior is similar to that reported for *Flabellina telja* Marcus and Marcus, 1967, by Ferreira & Bertsch (1972). The animal swims by lateral bending of the body (see Farmer, 1970, for a description of this method), as does *Coryphella iodinea* (Cooper, 1863) and *Flabellina telja* (MacFarland, 1966, and Marcus & Marcus, 1967).

1) **Holotype:** One intact whole specimen, 6.5 mm long preserved, deposited in the collections of the California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type no. 599.

2) **Paratypes:** One dissected radula (Figures *16* to *21*), mounted on a scanning electron microscope viewing stub, deposited in the collections of the California Academy of Sciences, Department of Invertebrate Zoology CASIZ Type no. 600 (CASIZ Type Slide Series no. 369).

3) An additional 5 entire specimens, also deposited at California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type Series, no. 601.

Description: The body lengths of 5 living animals (excluding the projecting cephalic tentacles) were 8, 9, 9, 10 and 15 mm. Body color a light orange, everywhere stippled with small white dots (Figure *3*). Cerata and rhinophores are light orange throughout most of their length, and tipped with white at their distal ends. The elongate tentacles (extending a third or more the length of the body; the 15-mm long specimen had cephalic tentacles measuring 6 mm long) are whitish throughout their entire length, as is also the extreme anterior region of the animal's body.

The spindle-shaped rhinophores have 15 to 19 perfoliations. Black eye spots, immediately behind the rhinophores, are visible in the preserved material.

There are 7 groups of cerata along each side of the dorsum; the rows do not arise from the flat sides of the body. Each group of cerata is attached to the dorsum by a single peduncle. The anterior liver has 3 groups of cerata, and is separated from the 4 cerata groups of the posterior liver by the cardiac prominence. The anterior and posterior cerata groups are the shortest, and the groups on either side of the cardiac prominence (numbers 3 and 4) are longest. Proceeding from the anterior to posterior, the numbers of cerata in each group are: 2, 4, 5, 5 or 6, 5, 4, 4.

The anus is located on the right side, below the cardiac hump, about ¼ the distance down the side. The reproductive openings are located on the right side, below the bases of the first and second ceratal groups.

The foot is set off from the side by a slight ridge, its anterior edge is bilabiate and set off from the mouth area by a small notch, and the anterior foot corners extend laterally in a crescent shape.

Radular formula 14 (1·1·1); the top three rachidian teeth, however, are missing (Figure *16*), and the lateral teeth occur only in rows 1 through 8. Lateral teeth have a rectangular base, with the side adjacent to the rachidian set at an oblique angle, slightly concave and coming to a sharp point, with about 9 irregular denticles along its length (Figure *17*). Often, the point is broken off. The rachidian tooth is chevron-shaped, with 6–8 denticles on each side (Figures *18* to *21*). Behind the plane of this main cutting edge is a large median cusp. The cusp has a knob (Figures *19* and *21*), which articulates into a depression in the back of the adjacent tooth (Figure *20*), and then rises to a point behind and between the two large uppermost denticles. The bases of the rachidian have flat outer sides, which come to a slight bump; the bases of the next tooth rest on these lateral bumps, enabling pressure applied on one tooth to be partially sustained by the following tooth.

Discussion: *Flabellina* ***stohleri*** can be distinguished readily from the six previously known species of Flabellinidae occurring in the Panamic province. None of the *Coryphella,* nor the one *Coryphellina,* species have cerata on peduncled supports. Moreover, *Coryphella californica* Bergh, 1904, has extremely long anterior foot corners and cerata; *Coryphella cynara* Marcus & Marcus, 1967, has long cerata almost ⅓ its body length, and purplish and red coloration on a bluish-white body; *Coryphella trilineata* O'Donoghue, 1921, has a translucent white body with 3 opaque white lines occurring along the length of its body; *Coryphella iodinea* (Cooper, 1863) has a rich purple and red color; *Coryphellina rubrolineata* O'Donoghue, 1929, has violet rings on the tentacles, rhinophores, foot corners, tail and cerata, and the rhinophores are papillated on the posterior surface (Marcus & Marcus, 1970c). None of these characteristics are shared by *Flabellina* ***stohleri***. The other *Flabellina, F. telja,* has a bluish-purple body; its radula has more teeth rows and a larger number of denti-

cles flanking the median cusp of the rachidian than does *F. stohleri*. The lateral teeth of *F. telja* lack denticles on the inner point, and its base has a concave posterior side (MARCUS & MARCUS, 1967: fig. 81); *F. stohleri* has denticles along one side of the point, and has a rectangular base.

This species is dedicated to our friend and mentor, Dr. Rudolf Stohler (editor of *The Veliger* and Research Zoologist, Emeritus, of the University of California, Berkeley), in admiration for his scientific achievements, his encouragement of molluscan studies and students, and his editorial zeal that has made *The Veliger* an outstanding international journal of malacozoology.

FACELINIDAE Odhner, 1939

Phidiana Gray, 1850

Phidiana ***lascrucensis*** Bertsch and Ferreira, spec. nov.

(Figures *4* and *22* to *27*)

Synonymy: *Phidiana* sp. Bertsch, 1971: 16
Phidiana sp. Williams and Gosliner, 1971: 33
Phidiana sp. Bertsch and Smith, 1973: 166

Material examined: 1) **Holotype:** One intact specimen (9 mm long, preserved) collected subtidally in about 2 meters of water in a small cove immediately north of the docks at Bahía Las Cruces (24°13′N; 110°05′W), Baja California del Sur, Mexico, on July 22, 1969, by Hans Bertsch. This specimen has been deposited in the collections of the California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type no. 602.

2) **Paratypes:** Five intact specimens, collected at the same time as the holotype. These specimens have been deposited in the collections of the California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type Series no. 603.

3) Three specimens collected intertidally at Bacochibampo Bay (27°55′N; 110°57′W), Sonora, Mexico, on December 26, 1970, by Hans Bertsch. This material, consisting of 1 intact animal (CASIZ Type no. 604) and 2 dissected radulae mounted on SEM stubs (CASIZ Type nos. 605 and 606, CASIZ Type Slide Series, nos. 370 and 371), has also been deposited in the collections of the California Academy of Sciences, Department of Invertebrate Zoology. This material is illustrated by the scanning electron micrographs, Figures *22* to *27*.

4) Dissected radula, mounted on microscope slide by Richard A. Roller, of specimen collected subtidally at N. Isla Cerralvo, July 29, 1969, by Hans Bertsch, deposited in California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type no. 607, CASIZ Type Slide Series no. 372.

5) Additional records (latitude and longitude of localities not given in this paper can be found in Bertsch, 1973, and Bertsch *et al.*, 1973):

Sonora, Mexico
- December 23, 1969, Bacochibampo Bay, 1 specimen, collected by Terrence M. Gosliner and Gary C. Williams

Baja California del Sur, Mexico
(collected by Bertsch:)
- July 3, 1969, Bahía Carisalito, 1
- July 12, 1969, Bahía Las Cruces, 1
- July 16, 1969, NW Isla Cerralvo, 1
- July 18, 1969, La Luna, 0.8 km north of Punta Gorda, 1
- July 22, 1969, S. end of Bahía Las Cruces, 1
- July 24, 1969, N. Isla Cerralvo, 2
- July 26, 1969, Bahía Las Cruces, 3
- July 29, 1969, N. Isla Cerralvo, 3
- July 24, 1972, S. end Isla Espíritu Santo, 2
- July 26, 1972, Bahía Carisalito, 3

Explanation of Figures *5* to *9*

The radula of *Thorunna* ***lapislazuli*** Bertsch & Ferreira, spec. nov. scanning electron micrographs by Hans Bertsch

Figure *5*: Whole view of radula × 100

Figure *6*: Center of radula, showing widened base and spike of innermost lateral tooth × 1 000

Figure *7*: Close-up view of innermost laterals × 2 325

Figure *8*: Inner lateral radular teeth, from center of upper right portion of Figure *5*, showing bicuspid tips, and small denticles on posterior surface of cusp × 1 000

Figure *9*: Outer lateral radular teeth from lower left portion of Figure *5*, showing many denticles on posterior surface of cusp, bicuspid tips, inter- and intra-row articulation, and elongate thin bases × 1 000

5

6

7

8

9

— [added in proof]
December 23, 1973, Rancho Notri, 12.8 km S. of Loreto (26°02′N; 111°21′W), 3
December 24, 1973, Juncalito, 19.2 km S. of Loreto, 5

(collected by Ferreira:)

July 13, 1971, Los Islotes, 3, in 10 m of water
August 10, 1973, Bahía Ventana, SE of Las Cruces, 3
August 10, 1973, Bahía Los Muertos, S of Bahía Ventana, 1
August 12, 1973, Bahía Eclipse, W side Isla Partida, 5
August 13, 1973, W side Isla San Francisco, 2
August 14, 1973, SE Isla San Diego (25°10′N; 110°44′W), 1
August 15, 1973, N Isla Santa Cruz, 3, in 20 m of water
August 16, 1973, Los Islotes, 1, in 10 m of water

— [added in proof]
November 24, 1973, S. Isla San Diego, 2, in 13 m of water
November 25, 1973, S. Isla Danzante (25°45′N; 111°14′W), 1, in 7 m of water

Southern Mexico and Central America
(collected by Ferreira:)
March 21, 1971, in Bahía Banderas, south of Punta Mita, Nayarit, Mexico, 1 (illustrated in Figure *4*)
February 24, 1972, Islas Tortugas, small group of islets on west side of entrance to Gulf of Nicoya, Costa Rica (9°27′N; 84°53′W), 12, in 3–7 m of water
January 24, 1973, El Zonte, Departamento La Libertad, El Salvador (13°30′N; 89°28′W), 3

There is an extensive intertidal and subtidal (to 20 m) collecting record for this new species on both sides of the Gulf of California, and along the open Pacific coast of Mexico and Central America. It currently has a known range of over 2600 km. The northern and southern extremes of the range are Bacochibampo, near Guaymas, Sonora, Mexico, and the entrance of the Gulf of Nicoya, Costa Rica.

Description: Length of living animal reaches a maximum of 22 mm. The lengths of 15 living animals were: 3, 5, 5, 8, 11, 12, 12, 13, 13, 13, 13, 18, 18, 19, and 22 mm. Table 1 compares the lengths and widths of 7 animals; this ratio is highly variable, and, similar to the body-length and tail-length ratio discussed by Edmunds (1964: 17–18), is not a good taxonomic character.

Body color orangish to orange-yellow or yellowish-white (Figure *4*); some had a faintly bluish-tinted white body. Anterior half of body often with a more heavily orange hue than the posterior region. Rhinophores and head tentacles orange, with a white tip; the white may not always be evident because of the animal's body parts being in various stages of regeneration. Numerous white specks (varying in number) scattered randomly along the dorsum area. The spindle-shaped cerata are transparent, the brown liver diverticulum clearly visible along the center of the individual ceras. Each ceras has an encircling white band slightly above the mid-region of its length, and a white tip. The white coloration varies in prominence because of varying degrees of regeneration. There are no red lines of color joining the cephalic tentacles, and no white lines on the dorsum nor foot.

Long cephalic tentacles (about ¼ to ⅓ the body length) are on the anterior corners (Table 1); cephalic region extends beyond the anterior margin of the foot.

Table 1

Body Length and Width and Cephalic Tentacle Length of Living *Phidiana lascrucensis* (in mm)

Length	Width	Cephalic Tentacles
22	—	5
13	1.5	3
12	2.0	—
8	1.5	—
11	2.5	3 - 3.5
13	3.0	—
12	3.5	—
18	3.0	—

Rhinophores are slightly shorter than the longest cerata, and have about 15 distinct annulations completely encircling the distal ⅔ of their length. The proximal ⅓ is smooth. Eye spots are clearly visible in living and preserved specimens, immediately behind the bases of the rhinophores.

Cerata in two main groups, an anterior with about 6–9 ceratal rows, and a posterior with about 8–15 ceratal rows (Table 2). There are 1–4 cerata in each row, the outer ones being shorter. The anterior and posterior cerata rows

Table 2

External Anatomical Characteristics of *Phidiana lascrucensis*

	Number of Ceratal Rows			Genital	
Preserved Length	Anterior	Posterior	Cerata per Row	Position [3]	Anus [4]
9mm [5]	7	8	2 - 4	6 - 7	4 - 5
4mm	6	9	1 - 3	—	—
6mm	7	11	2 - 4	6 - 7	6 - 7
7mm	6 + 7	8	2 - 4	6 - 7	4 - 5
11mm	9	15	1 - 4	7 - 8	—

[3] numbers indicate below which cerata rows in the anterior group the genital openings are located

[4] Numbers indicate between which cerata rows in the posterior group the anus is located

[5] Holotype specimen

of both groups are shorter than the middle cerata rows of both groups.

Anus on the dorso-lateral edge, in about the middle of the 2nd cerata group; genital openings along the side of the body, about ½ the distance from the dorsum to foot corners (Table 2), between the ultimate and penultimate cerata rows of the anterior group. Tip of penis (Figures *26* and 27) bears the generically-characteristic (Thiele, 1931: 458) spine.

Foot with a surrounding ridge around its edge; anterior region is not strongly dilated, and there are no broadly round, disc-like, nor crescent-shaped configurations resulting from contraction in preserved specimens.

Radula formula 15 (0·1·0), with 2 embryonic rows and 8–10 denticles on each side of the central cusp (Figures *22* to *25*). Base of tooth with a deep u-shaped notch, approximately 40% of the total length of the tooth. Muscular attachments join the top of the notch with the supportive tissue underlying the radula (Figures *23* and *24*). Just above the notch, the center of the tooth curves outward, then straightens out for the last ⅓ of the distance from the notch to the tip of the central cusp. Central cusp is not set off from the rest of the tooth, and one cannot clearly distinguish between denticles being on the cusp or along the sides (Figure *25*). Outer denticles largest, becoming smaller more or less evenly as they approach the tip of the main cusp. Tooth wear visible as broken or worn denticles and broken cusps (Figure *22*).

Jaws with 2 rows of denticles, 23–24 in the first row, 5–6 in the second row.

Explanation of Figures *10* to *15*

The radula of *Laila janssi* Bertsch & Ferreira, spec. nov.
scanning electron micrographs by Hans Bertsch

Figures *10* and *14*a, b are stereo pairs, published vertically instead of side-by-side. Resolution into a three-dimensional image can be easily accomplished by using a prism or the System Nesh (Klosterstraße 4-5, D-4400 Münster, West Germany), as described by Hayes (1973: 203 - 205). The vertical presentation of stereo pairs results in less eye strain while viewing than if the pairs were mounted laterally.

Figure *10*: Montage stereo pair of center of radula, an enlargement of the central portion of Figure *11* × 1 000

Figure *11*: Overall view of part of radula, showing relation between the pleural teeth and the laterals × 300

Figure *12*: Lateral teeth from left side of radula × 1 000

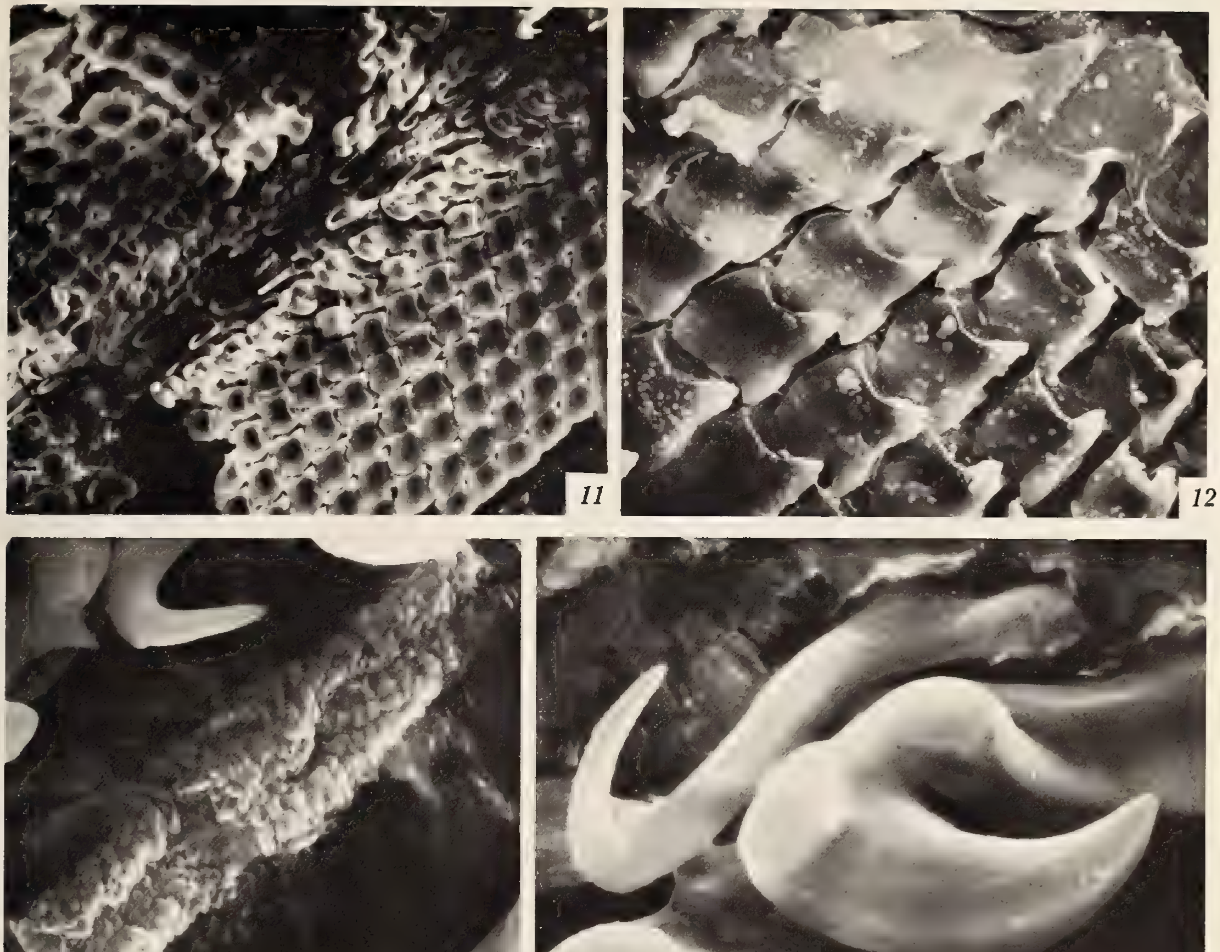
Figure *13*: Central rachidian plate, showing lack of any tooth, and the parallel ridges; enlargement of center of Figure *10* × 3 000

Figures *14*a, b: Stereo pair of pleural teeth, enlargement of upper right corner of Figure *10* × 3 000

Figure *15*: Enlargement of outer pleural tooth of Figure *14*, showing articulation between the bases of the pleural teeth × 3 630

[Figures *11* to *15*: see next Plate]

Figure 10



11 *12* *13* *14* a *15* *14* b

Discussion: There are three other species of *Phidiana* from the Pacific American coast: *Phidiana inca* (d'Orbigny, 1837); *P. lynceus* Bergh, 1867; and *P. pugnax* Lance, 1962. The main cusp of their radular teeth is distinctly set off from the rest of the tooth, and none of them have two rows of denticles on the jaws; these two internal characteristics separate *P. lascrucensis* as a new species. In addition there are numerous external characteristics distinguishing these three species from *P. lascrucensis.*

Phidiana inca (synonym: *Phidiana exigua* Bergh, 1898; cf. MARCUS & MARCUS, 1967) has white dots between the rhinophores, and a white or silver-white median stripe down the dorsum; the cerata have a white tip, with a subapical purple ring (BERGH, 1898: 549–550). *Phidiana lascrucensis* has no white stripe on the dorsum, and has a subapical white ring.

Phidiana lynceus (synonyms: *P. selenkai* Bergh, 1879, and *P. brevicauda* Engel, 1925; *P. lynceus* itself may possibly prove to be a synonym of *P. patagonica* (d'Orbigny, 1837)) has a vermilion red line joining the two oral tentacles, ending in a blotch at the middle of each tentacle; there is a mid-dorsal line of white from tail to rhinophores, bifurcating in front of rhinophores and then extending out to the tentacles; annulations on rhinophores are rarely complete anteriorly; tips of rhinophores and tentacles yellowish-brown (MARCUS, 1955 and 1957; EDMUNDS, 1964; and MARCUS & MARCUS, 1970 b). *Phidiana lascrucensis* has complete annulations on the rhinophores, and tips of rhinophores and tentacles are white.

Phidiana pugnax has 6 major ceratal groups; a red line runs across the front of the head to the midpoint of each tentacle; there is an opaque white spot on the anterolateral surface of the cerata, about ¾ of the way up. *Phidiana lascrucensis* has two major ceratal groups, no red line, and a white ring rather than a spot.

This species is named for the Las Cruces Biology Station (located at the type locality, Bahía Las Cruces), under the directorship of Dr. Rita Schafer, to acknowledge the assistance given numerous researchers of the southern Gulf of California fauna and flora by the staff of this marine station.

Behavioral observations: Speed of travel of normal-sized specimen, 90 mm per minute over a sandy substrate.

On July 22, 1969, Bertsch placed a living *Phidiana lascrucensis* in a weak solution of ethanol-sea water. The animal reacted violently, twisting and turning, and it autotomized many of its cerata. Despite being separated from the animal's body, these cerata continued flexing and bending for slightly more than 5 minutes. This independent movement of autotomized cerata has been reported for other nudibranchs, including the common eastern Pacific facelinid, *Hermissenda crassicornis* (Eschscholtz, 1831), by STASEK (1967: 11–15), who believes that the activity diverts the attention of a possible predator.

When *Phidiana lascrucensis* was mechanically stimulated, encountered a foreign substance while crawling, or was attacked by a predator, it bent its body back and forth laterally, in the swimming motion previously discussed for *Flabellina.* The locomotory effect of this bending was not much in the still waters of the aquarium, since the animal usually moved less than 10 mm. However, in its natural habitat, where water currents exist, this defensive reaction would probably be more effective.

The cephalaspidean opisthobranch, *Chelidonura inermis* (Cooper, 1863), successfully ate *Phidiana lascrucensis* in the aquarium, even though *P. lascrucensis* underwent the lateral body-bending as soon as *C. inermis* first touched it.

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Explanation of Figures *16* to *21*

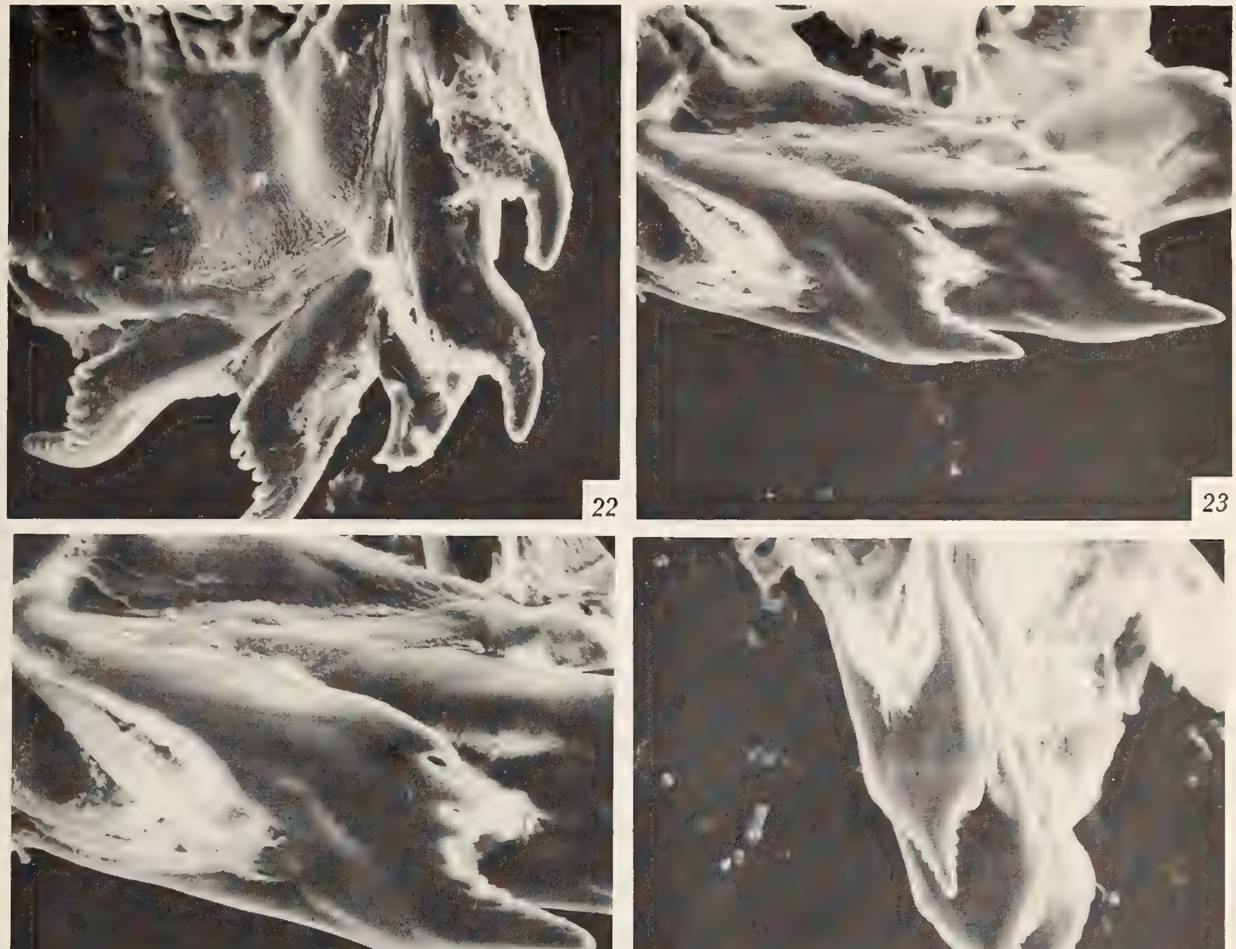
The radula of *Flabellina stohleri* Bertsch & Ferreira, spec. nov.
scanning electron micrographs by Hans Bertsch

Figure *16*: Side view of radula × 300
Figure *17*: Close-up view of lateral teeth; points broken off at upper right indicate tooth wear × 1 000
Figure *18*: Lateral view of first 3 rachidian teeth; cusp of lowest is broken off × 1 000
Figure *19*: Close-up view of 2nd rachidian tooth, showing lateral flange on which the base of the preceding tooth rests, and the large median cusp separate from the plane of the denticles × 3 000
Figure *20*: Dorsal view of rachidian tooth, showing depression on back of tooth into which median cusp of following tooth fits. × 2 000
Figure *21*: Ventral view of rachidian, showing median cusp set off distinctly from the rest of the tooth × 1 800

Explanation of Figures *22* to *27*

The radula of *Phidiana lascrucensis* Bertsch & Ferreira, spec. nov.
scanning electron micrographs by Hans Bertsch

Figure *22*: Lateral view of radula, showing bend of rachidian cusp × 300
Figure *23*: Radula of another specimen; note that main cusp is not set off from the rest of the tooth × 300
Figure *24*: Enlargement of Figure 23 × 475
Figure *25*: Same area as shown in Figure *23*, but from a different angle and at lower magnification × 255
Figure *26*: Penis × 100
Figure *27*: Tip of penis, showing spine × 300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Recognition and Distribution of *Mytilus condoni* Dall, a Unique Pliocene and Pleistocene Bivalve from the Pacific Coast [1]

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(1 Plate)

INTRODUCTION

Mytilus condoni Dall (1890), a uniquely sculptured Pliocene mytilid from western Washington, has been a poorly known, if not doubtful, species ever since its description. Study of specimens from the recently rediscovered type locality now permits confident recognition of *M. condoni*. This species ranged as far south as central California during the late Pliocene. The broad distribution and late Pliocene and early Pleistocene age of known occurrences of this species point to its potential usefulness in provincial correlation.

Mytilus condoni was originally collected at Willapa [Shoalwater] Bay, southwestern Washington, and was described in a letter to the editor of the Nautilus by W. H. Dall (1890) in which he summarized some conchological observations in Oregon. The obscure titling of Dall's report, coupled with the facts that a holotype was not designated (Boss *et al.*, 1968: 87) and the species had not previously been illustrated, left the identity of this uniquely sculptured *Mytilus* in doubt. Later Dall (1904: 113) seems to have regarded this species as either a synonym or a closely related descendant of *M. middendorffi*, a widespread rugose species of middle Miocene age (Allison & Addicott, 1973), in stating that the latter "... is represented in the Pliocene of Oregon by *Mytilus condoni* Dall ...". The obscurity of the original publication is evidenced by Grant & Gale's (1931) comment that they were unable to find a description of *M. condoni* and by Weaver's (1942) omission of this species from his catalogue of Tertiary fossils of Oregon and Washington. Much later, Hertlein (*in* Manning & Ogle, 1950: plt. 8) regarded a mytilid from Humboldt County, California, now known to be this species, as undescribed but allied to *M. middendorffi;* he further noted that "This specimen may be similar to '*Mytilus condoni* Dall' which was mentioned in an earlier publication of the Nautilus (1911?), by Dall as occurring in Oregon." At about the same time identical material from this northern California locality was described as *M. highoohiae* Mandra (1949: 104–105; fig. 1). Additional records of this species from localities in Humboldt County are recorded herein.

Reconnaissance of flat-lying siltstone and silty sandstone exposed in cliffs along the north shore of Willapa Bay has relocated what is here considered to be the *Mytilus*-bearing bed from which this species was originally collected. The fossils are from an unnamed unit mapped by Huntting *et al.* (1961) as Quaternary terrace deposits. Although now readily accessible by paved road, these strata were difficult to reach and apparently unknown to three generations of paleontologists until construction of the coastline alignment of State Route 105 during the early 1960's. With the rediscovery of the type locality and availability of topotypic material, the finely sculptured *M. condoni* can be readily distinguished from the rugose middle Miocene species *M. middendorffi* Grewingk with which it has been confused (Dall, 1904; Hertlein *in* Manning & Ogle, 1950) as shown by Figures *1* to *9*. This discovery also shows that *M. condoni* is conspecific with the later described *M. highoohiae* Mandra (1949), which was based on material from the Pliocene Falor Formation of Manning & Ogle (1950) of northwestern California. More importantly, this uniquely ribbed mytilid is widespread in shallow-water rocks of late Pliocene and early Pleistocene

[1] Publication authorized by the Director, U. S. Geological Survey

age and serves, therefore, as a useful species in stratigraphic correlation.

This note designates and illustrates type material for *Mytilus condoni,* designates the neotype locality, and considers the stratigraphic significance of this species. The original description is reprinted herein so as to make it more widely available.

SYSTEMATIC PALEONTOLOGY

Mytilus Linnaeus, 1758

Mytilus condoni Dall, 1904

Figures *3–9*

1890. *Mytilus condoni* Dall, Nautilus 4 (8): 88 - 89
1949. *Mytilus highoohiae* Mandra, Journ. Paleont. 23 (1): 104 - 105; fig. 1
1950. *Mytilus* aff. *middendorfi* Grewingk, n. sp., Manning & Ogle, Calif. Div. Mines Bull. 148, plt. 8

Neotype (here designated): U. S. National Museum No. 647272

Neotype locality: USGS Cenozoic loc. M5219, near base of cliff on north side of State Route 105, 1020 m S., 900 m W. of NE. cor. sec. 5, T. 14 S., R. 10 W., Bay Center 7½′ quad., Pacific County, Washington. *Mytilus*-bearing beds about 3.6 m thick overlying a 60 cm-thick *Macoma* bed. Unnamed formation of late Pliocene age.

Original description: "The most remarkable, and only new form in this bed [at Shoalwater Bay, Washington] is a fine *Mytilus* as large as *M. californicus* but distinguished from all other species of the genus by its surface which resembles that of *M. edulis* superimposed upon which are a few strong divaricating ridges extending from about the middle of the valves toward the posterior extreme. Many species have the surface covered with fine divaricating lines but I believe there is none known in which there are a few strong distant ridges, perhaps not exceeding half a dozen on the surface of a shell six inches in length, and having otherwise the form and aspect of a giant *M. edulis.* For this interesting species I propose the name of *M. condoni* in honor of its discoverer" (Dall, 1890: 88–89).

Discussion and Comparisons

Mytilus condoni is characterized by a network of moderately fine, divaricating ribs that bifurcate along the median line of the valves. The ribs are of variable strength but are best developed on the medial and dorsal parts of the valves and tend to reach the ventral margin at a much later stage of growth than the dorsal margin. The ribs are relatively flat-topped and are much broader than the interspaces. They are much more numerous than suggested by Dall (1890: 89); in fact, the very nature of Dall's description of this species leads to the speculation that it was made from memory and not with material at hand. The early growth stages are characterized by a smooth surface; the divaricate rib pattern develops after a length of about 25 mm is attained. On a few specimens, however, the smooth surface is maintained until a much later stage in growth (Figure *3*). The shell margin is smooth except for the development of a few teeth in the umbonal region.

Assignment to *Mytilus* is suggested by the similarity of internal morphology to that of the cosmopolitan species *M. edulis.* On the interior part of the valve, the dentition, position of the anterior adductor muscle scar, and outline and position of the posterior retractors are all remarkably similar to *M. edulis.* The similarity (Figure *5*) of external features to *M. edulis* has already been noted by Dall (1890).

This species was later confused with *Mytilus middendorffi,* a coarsely plicate species of middle Miocene age (Figures *1* and *2*), by its describer (Dall, 1904). One can surmise that in the absence of designated and illustrated type material and perhaps also because the original specimen may not have been available, the critical features that readily distinguish this unique species from all other Pacific coast mytilids, as originally noted by Dall (1890), were overlooked in his later publication. An additional problem was the difficulty, until recently (Hall, 1958), of identifying *M. middendorffi* because only Grewingk's original line drawings were available and these appeared in obscure or difficult to obtain publications (Grewingk, 1850; Gratacap, 1912; Slodkewitsch, 1938). Actually, the two divaricately ribbed mytilids can be readily distinguished from each other as shown by Figures *1–9*. *Mytilus condoni* is characterized by a pattern of moderately fine divaricate ribbing, whereas *M. middendorffi* has a few rugose plicae that produce undulatory deflections of the plane of commissure. The sculpture of *M. middendorffi* consists of two main folds and, usually, finer folds that branch off of the main dorsal fold in the posterior dorsal area of the valves.

Two paleontologists working with specimens of *Mytilus condoni* from northwestern California independently regarded their material as representing a new species (Mandra, 1949, and Hertlein *in* Manning & Ogle, 1950). Mandra (1949: 104) endeavored to compare his specimens with the known Cenozoic *Mytilus* from the Pacific coast;

he did not, however, include *M. condoni* among the 23 species that were listed as having been reviewed. HERTLEIN (*op. cit.:* plt. 8) mentioned the possible similarity to *M. condoni* but regarded Dall's species as an unavailable name stating that "No description or figures of '*M. condoni*' are available . . ."

AGE AND CORRELATION

Although DALL (1890) originally described the occurrence of *Mytilus condoni* as Pliocene, he did not present supporting paleontologic evidence. The only subsequent mention of the age of unnamed unit along the north shore of Willapa Bay from which specimens of *M. condoni* have been collected was by MACNEIL (1965: G33), who considered these beds as probably Pleistocene, again without paleontologic documentation.

The shallow-water assemblage with which *Mytilus condoni* is associated at Willapa Bay (USGS locs. M1681, M1682, M5219) is dominated by living species, almost exclusively bivalves. Included are *Mya japonica* Jay, *Clinocardium nuttalli* (Conrad), *Macoma inquinata* (Deshayes), and *M. brota* (Dall)?. There is one extinct species in the assemblage—*Macoma* n. sp.? Addicott (1969)—a large tellinid that occurs in late Pliocene assemblages from the Merced Formation (USGS loc. M1715) and the Purisima Formation (USGS loc. M3618) in central California. Accordingly, the age of this species at the neotype locality is considered to be late Pliocene.

In the Falor Formation of MANNING & OGLE (1950) of Humboldt County, northern California, *Mytilus condoni* (Figure 7) occurs with the Pliocene cardiid *Clinocardium meekianum* (Gabb), together with some of the still-living species with which it is associated at the type locality [*Mya japonica* Jay, *Clinocardium nuttalli* (Conrad), and *Macoma inquinata* (Deshayes)]. FAUSTMAN (1964; 111) compared the fauna of the Falor with assemblages from the middle and upper parts of his Rio Dell Formation of the nearby Eel River basin. This correlation implies a generalized late Pliocene age for this occurrence of *M. condoni*. This species occurs in recent collections from the stratigraphically higher Carlotta Formation of OGLE (1953) of the Eel River sequence. It is associated with an unpublished molluscan assemblage of still-living species (F. H. Kilmer, written commun., June 5, 1973) suggestive of a provincial early Pleistocene age.

On the San Francisco Peninsula near San Bruno, California, *Mytilus condoni* (Figure 9) occurs in the lower part of the Merced Formation with *Ophiodermella graciosana* (Arnold) and other species indicative of a provincial late Pliocene age (Thomas Yancey, written commun., December, 1971).

In summation, *Mytilus condoni* has an extensive geographic range along the Pacific coast, and in each of the areas from which it is known, it occurs with mollusk assemblages of provincial late Pliocene or early Pleistocene age. For these reasons, and because of its especially distinctive sculpture, *M. condoni* appears to be an excellent index fossil for strata of this age along the Pacific coast. Its occurrences in northern California and western Washington are in bivalve assemblages suggestive of low intertidal or uppermost inner sublittoral depths in embayed or otherwise protected marine environments.

Explanation of Figures *1* to *9*

Figure *1*: *Mytilus middendorffi* Grewingk. USNM 647269. USGS Cenozoic loc. M3614. Temblor Formation, middle Miocene. San Benito County, California.

Figure *2*: *Mytilus middendorffi* Grewingk. USNM 647270. USGS Cenozoic loc. M3614. Temblor Formation, middle Miocene. San Benito County, California.

Figure *3*: *Mytilus condoni* Dall, USNM 647271. USGS Cenozoic loc. M1682. Unnamed formation, late Pliocene. Willapa Bay, Washington. (× 1½)

Figure *4*: *Mytilus condoni* Dall. Neotype. USNM 647272. USGS Cenozoic loc. M5219. Unnamed formation, late Pliocene. Willapa Bay, Washington.

Figure *5*: *Mytilus condoni* Dall. USNM 647273. USGS Cenozoic loc. M5219. Unnamed formation, late Pliocene. Willapa Bay, Washington. (× 2½)

Figure *6*: *Mytilus condoni* Dall. USNM 647274. USGS Cenozoic loc. M5219. Unnamed formation, late Pliocene. Willapa Bay, Washington. (× 1½)

Figure *7*: *Mytilus highoohiae* Mandra. Holotype. UCMP loc. A4234. Falor Formation of MANNING & OGLE (1950), late Pliocene. Humboldt County, California.

Figure *8*: *Mytilus condoni* Dall. USNM 647275. USGS Cenozoic loc. M5219. Unnamed formation, late Pliocene. Willapa Bay, Washington.

Figure *9*: *Mytilus condoni* Dall. UCMP 10928. UCMP loc. D3364. Merced Formation, late Pliocene. San Mateo County, California.

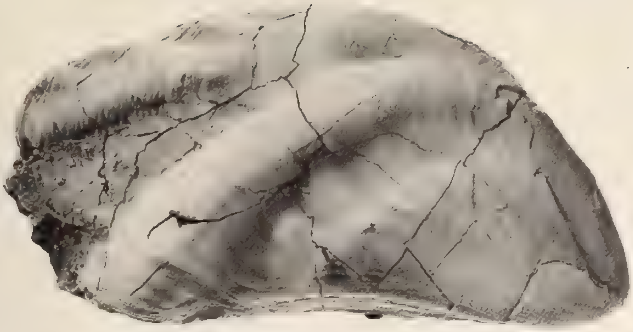

Figure *1*

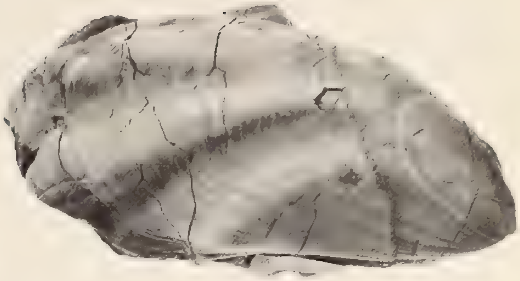

Figure *2*

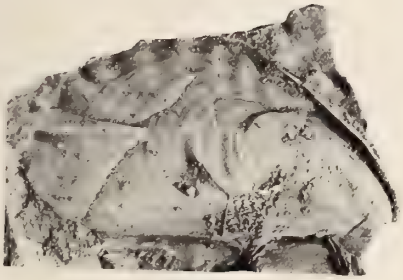

Figure *3*

Figure *4*

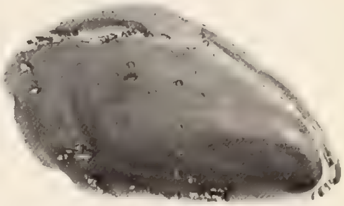

Figure *5*

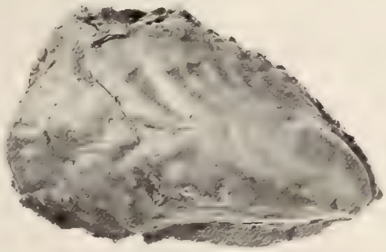

Figure *6*

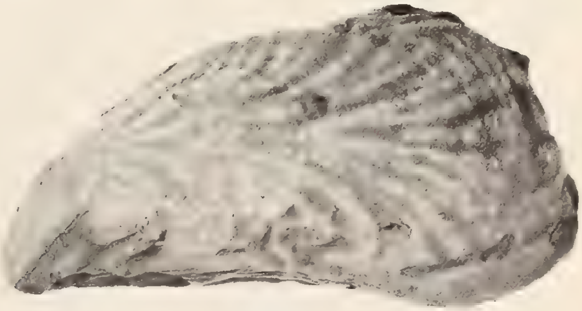

Figure *7*

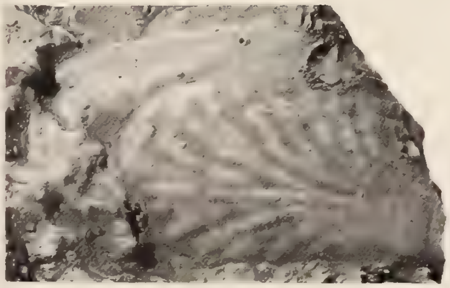

Figure *8*

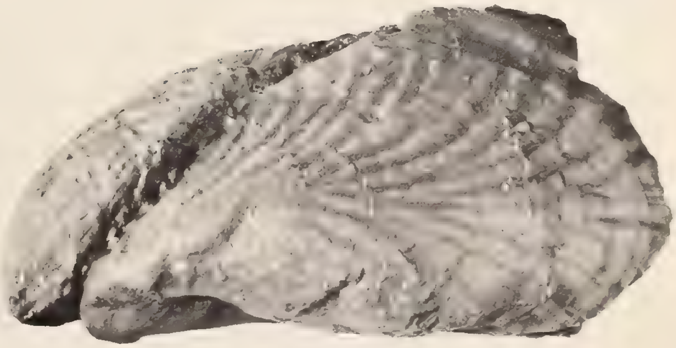

Figure *9*

ACKNOWLEDGMENTS

I am indebted to Thomas Yancey, University of Malaya, for stratigraphic data on central California occurrences of *Mytilus condoni* and for material from the Merced Formation illustrated in this report. F. H. Kilmer and Samuel Morrison, Humboldt State University, furnished unpublished data on the occurrence of this species at localities in the Eel River basin, California. Helpful discussions of the taxonomy of this species were held with Richard C. Allison and F. Stearns MacNeil. Eugene V. Coan and Ellen J. Moore kindly read the manuscript and offered critical comments. Photographs are by Kenji Sakamoto. Most of the illustrated material was prepared by John W. Miller.

FOSSIL LOCALITIES

United States Geological Survey (USGS):

M1681. Cliff on north side State Route 105, approximately 45 ft[1] (13½ m) above highest reaches of tide. 1 700 ft (510 m) S of NE cor. sec. 6, T. 14 N., R. 10 W., Bay Center 7½′ quad., Pacific County, Washington. Unnamed formation, late Pliocene.

M1682. Cliff on north side of State Route 105, approximately 37 ft (11.1 m) above highest reaches of tide; 3 400 ft (1020 m) S., 2 200 ft (660 m) E. of NW. cor. sec. 5, T. 14 N., R. 10 W., Bay Center 7½′ quad., Pacific County, Washington. Unnamed formation, late Pliocene. Same as loc. M5219.

M1715. Cut and pipeline trench on north side of Arastradero Road, 1 200 ft (360 m) W. of intersection with Page Mill Road, Palo Alto 7½′ quad., Santa Clara County, California. Merced (?) Formation, late Pliocene.

M3614. Concretionary sandstone in cliff on west side of Silver Creek, 1 700 ft (510 m) N., 900 ft (270 m) E. of SW. cor. sec. 5, T. 17 S., R. 12 E., New Idria 15′ quad., San Benito County, California. Temblor Formation, middle Miocene.

M3618. Seacliff at northwest end of New Brighton Beach State Park near Capitola. Soquel 7½′ quad., Santa Cruz County, California. Purisima Formation, late Pliocene.

M5219. Near base of cliff on north side of State Route 105, 3 400 ft (1020 m) S., 3 000 ft (900 m) W. of NE. cor. sec. 5, T. 14 S., R. 10 W., Bay Center 7½′ quad., Pacific County, Washington. *Mytilus*-bearing beds about 12 feet (3.6 m) [in] thick[ness] overlying a 2-foot-thick (60 cm) *Macoma* bed. Unnamed formation, late Pliocene. Same as loc. M1682.

California University, Berkeley (UCMP):

1719. On the cliff ½ mi. (800 m) due northeast of Mussel Rock. along east side NW¼ sec. 15, T. 3 S., R. 6 W., San Mateo County, California. Merced Formation, late Pliocene.

A4234. Mad River road near mouth of Canon Creek, grid zone G coordinates 729 and 2045.3, Blue Lake 15′ quad. (1943 edition), Humboldt County, California. Falor Formation of Manning & Ogle (1950), late Pliocene.

D3364. On southwest side of small hill nearly 100 ft (30 m) NE of Gellert Boulevard just north of intersection with Verducci Drive, 4 750 ft (1425 m) S., 200 ft (60 m) W. of lat 37°40′N. and long 122°27.5′W., San Francisco South 7½′ quad., San Mateo County, California. Merced Formation, late Pliocene.

D4090. Merced Formation, northern San Francisco Peninsula [no locality coordinates available]. Field loc. JGM 69017.

D5927. Foot of hillside cut on north side of Twelvemile Creek approximately 1 500 ft (450 m) W. of U. S. Route 280 interchange, 7 750 ft (2325 m) S., 1 450 ft (435 m) E. of lat 37°40′N. and long 122°27.5′ W., San Francisco 7½′ quad., San Mateo County, California. Altitude about 420 ft (126 m). Merced Formation, late Pliocene.

California Academy of Sciences (CAS):

28905. A ledge in place by beach about ½ mi. (800 m) north of Mussel Rock. Lower part of the Merced Formation, late Pliocene. [in NW¼ sec. 14, T. 3 S, R. 6 W., San Mateo County, California.]

Humboldt State University (HSU):

994. Gulch along eastern boundary of ranch at "Stone" railroad crossing, 1 200 ft (360 m) S., 100 ft (30 m) W. of NE. cor. sec. 31, T. 2 N., R. 1 E., Fortuna 15′ quad., Humboldt County, California. Near the base of the Carlotta Formation of Ogle (1953), early Pleistocene.

1180. From trenches in topographic saddle immediately west of Maple Creek School-Korbel road, 1 800 ft (540 m) N., 2 200 ft (660 m) W. of SE. cor. sec. 30, T. 4 N., R. 3 E., Blue Lake 15′ quad., Humboldt County, California. Falor Formation of Manning & Ogle (1950), late Pliocene.

[1] In accordance with Veliger editorial policy, all quoted measurements will be given as originally cited with the metric equivalent in parentheses immediately following.

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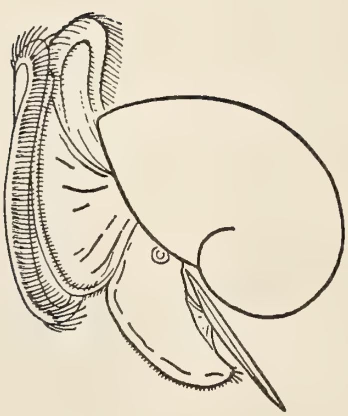

On the Affinities of *Humboldtiana fullingtoni* Cheatum, 1972

(Mollusca : Pulmonata : Helminthoglyptidae)

BY

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(2 Plates; 1 Table; 2 Text figures)

INTRODUCTION

Through the courtesy of the late Dr. E. P. Cheatum, it was possible to dissect a paratype of *Humboldtiana fullingtoni* Cheatum (1972). The specimen is catalogued as Field Museum of Natural History 170054. In structure of the jaw (Figure *3*) and radula (Figures *6–14*), *H. fullingtoni* resembles most closely *H. texana* Pilsbry, 1927. The shell of *H. texana* has prominent granulations, is much smaller, has a higher whorl count, and the genitalia (see Pilsbry, 1939: 407; figures 272, 8, 9, 10) differ most obviously in the mucus glands being situated well above the dart sacs. *H. fullingtoni* has a smooth, relatively large shell, the lowest mean whorl count known in the genus (see Table 1), and the mucus glands are situated only slightly above the dart sacs. On the basis of genital structures, so far as those of other species have been illustrated, *H. nuevoleonis* Pilsbry, 1927 from Mexico (see Pilsbry, 1948: 191; fig. 3, A) has very similar terminal female genitalia and the penial structures of the Mexican *H. striata* Burch & Thompson (1957, plt. V, D) are quite comparable. On the basis of the current criteria for species recognition, there is no question but that *Humboldtiana fullingtoni* is a valid taxon. Sufficient data has now accumulated concerning the structures of *Humboldtiana* to permit some comments concerning the patterns of variation and to suggest further areas for investigation. These follow the more formal descriptive and comparative notes.

The scanning electron microscope photographs (Figures *3–14*) illustrating this paper were made during cooperative research with the American Dental Association Research Institute. I am indebted to Mr. George Najarian, Mr. John Lenke, and Dr. Harvey Lyon of their staff for invaluable assistance in this work. The quality of the prints is due to the skill and patience of Fred Huysmans, Field Museum of Natural History. Text figures 1 and 2 were drawn by Claire Kryczka. For help with various phases of specimen, figure and manuscript preparation, I am indebted to Ms. Jayne Freshour, Mrs. Dorothy Karall and Ms. Barbara Walden.

PREVIOUS STUDIES

The basic literature on *Humboldtiana* and preliminary outline of variation patterns have been developed by Pilsbry (1927, 1935, 1939 and 1948). The many scattered species descriptions are tallied in a useful check list by Burch & Thompson (1957: 1–2), who also dissected and figured three new species from Central Mexico. Their map of distribution (p. 3) is but little altered by subsequent reports. Pratt (1971) and Cheatum (1972) each described single new species. Bequaert & Miller (1973: 27–32; fig. 3) reviewed the distribution of *Humboldtiana,* synonymized *H. edithae* Parodiz, 1954 with *H. chisoensis* Pilsbry, 1927, and clarified the type localities for several Texas species. The above references provide entre to the descriptive literature.

Pilsbry (1927: 166–168 and 1948: 186) pointed out the most obviously variable feature of the anatomy, the distance relationship between dart sacs and mucus glands, plus the presence of what he called "a small chamber at the apex" of the penis. Subsequently Burch & Thompson (1957: 2) suggested that these features delineated two groups of species, "which should perhaps be designated as subgenera." Pratt (1971: 434) reported that a new species, *Humboldtiana agavophila,* had the dart sac-mucus gland character of one group and the penial structure of the other.

At present, there are 25 described species of *Humboldtiana,* two of which [*H. hoegeana* (von Martens, 1890)

and *H. montezuma* Pilsbry, 1940] have subspecies. Of these, 15 species and one subspecies have been dissected, mostly only on the basis of one population. *Humboldtiana "humboldtiana* (Pfeiffer)" and *H. potosiana* Pilsbry, 1927 were dissected in the last century (see PILSBRY, 1927: 173–178 for references); *H. buffoniana* (Pfeiffer, 1845), *H. texana* Pilsbry, 1927, *H. chisoensis* Pilsbry, 1927, and *H. ultima* Pilsbry, 1927 by PILSBRY (1927); *H. nuevoleonis* Pilsbry, 1927, *H. montezuma* Pilsbry, 1940, *H. montezuma inferior* Pilsbry, 1948, *H. chrysogona* Pilsbry, 1948, and *H. fortis* Pilsbry, 1940 by PILSBRY (1948); *H. fasciata* Burch and Thompson, 1957, *H. globosa* Burch and Thompson, 1957 and *H. striata* Burch and Thompson, 1957 by BURCH & THOMPSON (1957); *H. agavophila* Pratt, 1971 by PRATT (1971); and *H. fullingtoni* Cheatum, 1972 in this report.

GROSS ANATOMY OF *Humboldtiana fullingtoni*

External features and color of the living animal were reported by CHEATUM (1972). The discussion here is limited to internal anatomy with emphasis on those features potentially with high information value in interpreting the phylogeny of the genus.

Pallial region, (Figure 1, b) differing from that of *Humboldtiana ultima* (see PILSBRY, 1927: plt. 14, fig. 6 and PILSBRY, 1939: 405; fig. 270, 6) in having a shorter distance from the anterior kidney (K) margin to the mantle collar (MC), with pulmonary venation (HV) more diffuse and less concentrated. The posterior angulation shown in the kidney of *H. ultima* is greatly reduced in *H. fullingtoni*. Quite possibly this difference is partly an artifact of differential retraction. During deep retraction into the shell, the pallial organs can be jammed and partly distorted. If the dissected specimen of *H. ultima* had been preserved in a contracted position, then the sharp posterior angulation might be the result of such distortion. Much more significant is the fact that the kidney (K) in *H. fullingtoni* is shorter and broader than that of *H. ultima*. The heart (H) is about half the length of the kidney and the intestinal loop (I) deeply intrudes onto the pallial margin. Cutting the ureter (KD) at its point of reflexion enabled illustrating the quite broad expanse of lung roof between kidney and hindgut (HG). The excretory pore (KX) continues as a narrow channel through the pneumostome, with the anal opening (A) lateral and above the pneumostome.

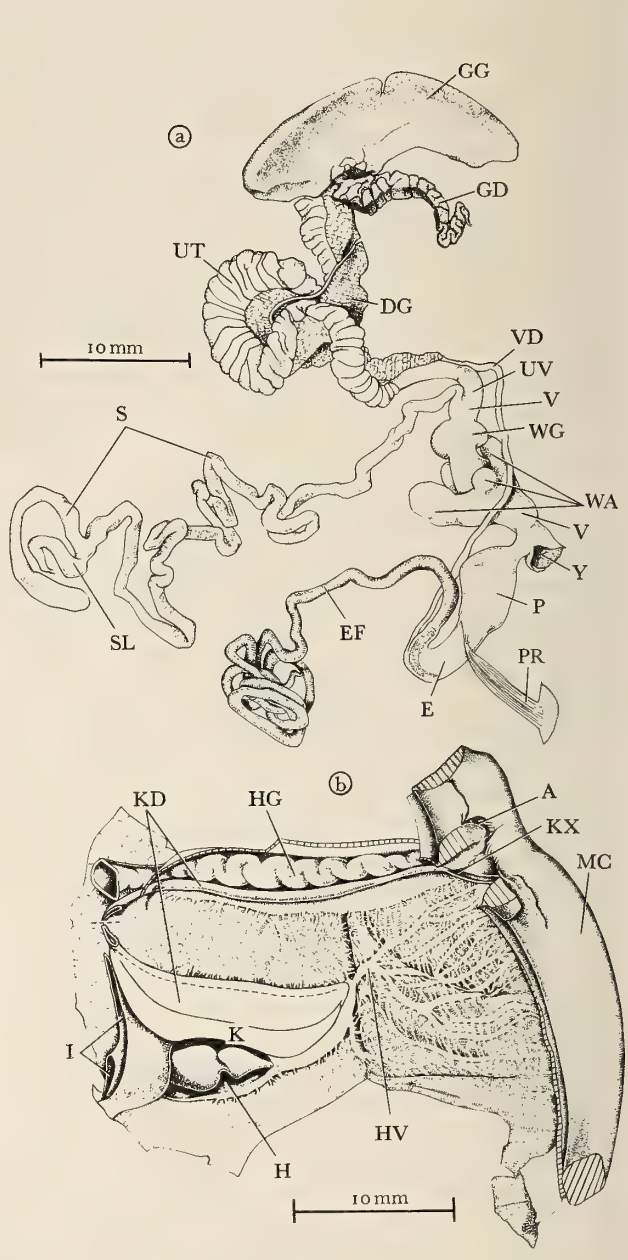


Figure 1

Humboldtiana fullingtoni Cheatum, 1972

Paratype. FMNH 170054: a - genitalia with ovotestis omitted; b - pallial complex with ureter (KD) severed posteriorly to show relationship of kidney (K) and hindgut (HG). Scale line = 10 mm

The excised genitalia (Figure 1, a) show the features characteristic of *Humboldtiana*—mucus gland (WG) bulge above the four unequal sized dart sacs (WA), highly convoluted and elongated spermathecal shaft (S) with subapical caecum (SL), very long epiphallic flagellum (EF), penial retractor muscle (PR) inserting around the head of the penis-epiphallus junction, and swollen epiphallus (E). The dart sacs are unequal in size. The mucus gland swelling is located only slightly further up the vagina (V) than the length of the longest dart sac. The hermaphroditic duct (GD), albumen gland (GG), prostatic (DG) and uterine (UT) sections of the functional spermoviduct, vas deferens (VD), and free oviduct (UV) show no unusual features.

When opened longitudinally (Figure 2, *a*), the penis (P) and epiphallus (E) show sharply different structures. The epiphallus has four corrugated longitudinal ridges that continue into the verge (PV) through a narrow pore. The demarcation between epiphallus and verge is marked by an apparent change from corrugated to smooth pilaster surfaces. This results from an accessory membrane that lines the inside of the verge from its tip to the epiphallic termination. This membrane is attached firmly only at the tip and start of the verge, forming a loose covering in the midregion. The corrugated ridges of the epiphallus extend unchanged to the verge tip, where they emerge as broad flap-like processes. In the dissected specimen of *H. fullingtoni,* these appear as simple undulations rather than the clear projections seen in such species as *H. fasciata* (see BURCH & THOMPSON, 1957: plt. V, *a–d*). The verge in at least this species is thus an extended section of the epiphallus. An inner membrane has been added, which forms an internal "ring chamber" to the verge. In its probably somewhat contracted position, the verge is about 2.6 mm long, or approximately half the total length of the penis chamber. There is a huge, relatively high, transverse pilaster (Figure 2, a, PP) that forms a "donut-shaped" structure around the verge tip. Much lower and broader traces of two additional pilasters lead off from the main one, narrowing as they approach and then enter the atrium (Y). The proportionately shortened nature of the penis compared with other *Humboldtiana* (see Table 1) probably explains the lateral distortion of the pilasters. A similar pattern is seen in *H. striata* BURCH & THOMPSON (1957, plt. V, D).

The terminal female genitalia are compacted (Figure 1, a), with the unaltered vaginal area very short below the dart sacs (WA) and with the mucus glands (WG) situated only slightly above the apex of the largest dart sac. Internally (Figure 2, b) there are three different zones of pilasters—simple longitudinal ones in the atrium (Y) and vagina (V), higher and fewer in the dart sac zone, with

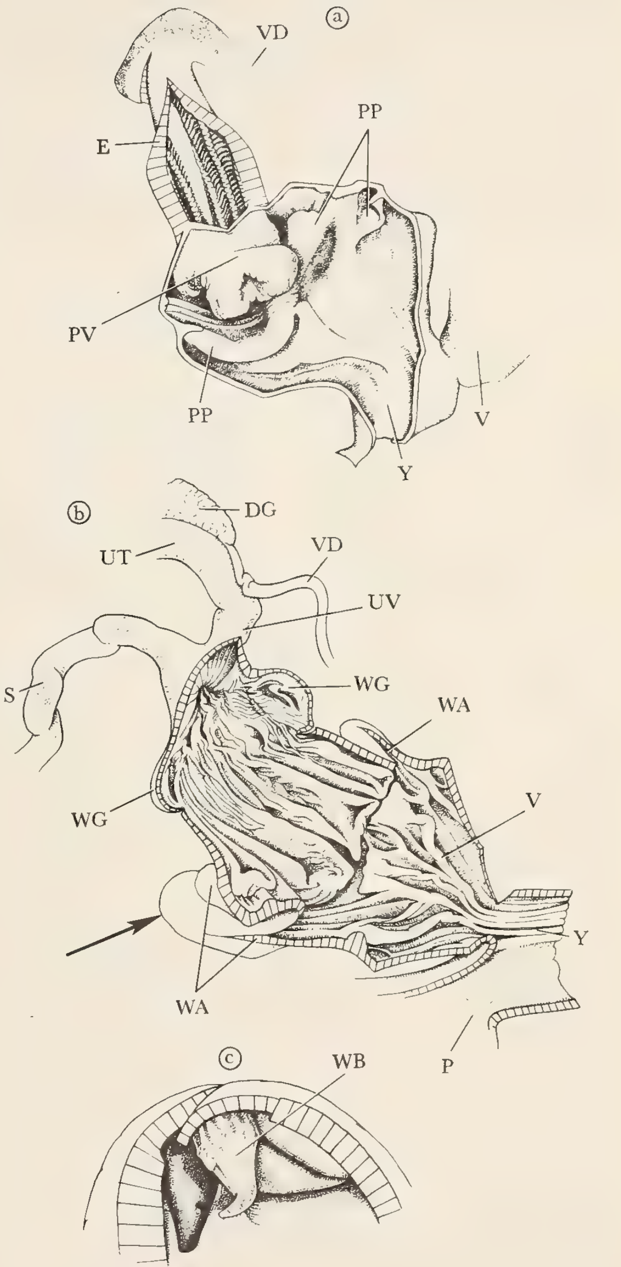


Figure 2

Humboldtiana fullingtoni Cheatum, 1972

Paratype. FMNH 170054: a - interior of penis and epiphallus; b - interior of terminal female genitalia; c - dart (WB) inside dart sac (WA) indicated by arrow in b. All greatly enlarged over scale shown in Figure 1 - a

Table 1

Variation in dissected species of *Humboldtiana*

Species	Diameter of shell (mean and range)	Whorl count (mean and range)	Penis length (mm)	Mucus gland	Free vagina
Humboldtiana					
H. fortis	36.2(34.9 - 37.4)	$4\frac{3}{4}$ – ($4\frac{1}{8}$ - $5\frac{1}{8}$)	8 - 12	S	M - L
H. montezuma	49.6(47.8 - 51.4)	$4\frac{1}{2}$	11	S	M
H. nuevoleonis	36.2(30.4 - 44.8)	$4\frac{1}{2}$ – ($4\frac{1}{4}$ - 5)	8 - 9	S - L	L
H. chrysogona	26.5	$4\frac{1}{2}$	9	S	L
H. montezuma inferior	34.2(30.5 - 38.5)	$4\frac{1}{2}$ – ($4\frac{1}{3}$ - $4\frac{1}{2}$)	8	S	S
H. buffoniana	39.6(37.4 - 42.0)	$4\frac{3}{8}$ – ($4\frac{1}{4}$ - $4\frac{1}{2}$)	10 - 12	S	S
H. fasciata	39.8(39.2 - 40.4)	$4\frac{1}{4}$	17 - 21	L	M
H. globosa	33.0	$4\frac{1}{4}$	12	M	S
H. chisoensis	31.0(25.0 - 33.9)	$4\frac{1}{4}$ – (4 - $4\frac{1}{2}$)	7	L	L
H. potosiana	25.0	$4\frac{1}{4}$	—	S	S
H. texana	24.4(20.5 - 26.3)	$4\frac{1}{8}$ – ($3\frac{7}{8}$ - $4\frac{1}{2}$)	7	L	M - L
H. striata	34.1(28.1 - 38.0)	$4\frac{1}{8}$ – ($3\frac{3}{4}$ - $4\frac{1}{4}$)	7 - 8	S	S
H. agavophila	??? (23.6 - 29.4)	4 – ($3\frac{7}{8}$ - $4\frac{1}{2}$)	6(?)	M	L
H. ultima	26.9(23.3 - 30.3)	4 – ($3\frac{2}{3}$ - $4\frac{1}{4}$)	7	S	L
H. fullingtoni	36.7(35.2 - 38.1)	$3\frac{3}{4}$ – ($3\frac{1}{2}$ - 4)	6	S	S

the latter then fragmenting into numerous high and thin pilasters that extend through the mucus gland zone before part of them rejoin into pilasters that extend up into the spermathecal shaft (S). A cluster of even finer and more numerous pilasters extends into the base of the free oviduct (UV). By opening the largest of the four dart sacs (Figure 2, c), the shape of the dart papilla (WB) with its curved tip is revealed. The illustrated dart sac is indicated by the arrow in Figure 2, b. Loose calcareous matter was associated with mucus in the glandular sides of the pocket shielding the dart papilla, but no stiffening of the papilla or indication of a hard dart could be found in any of the four dart sacs. Pilsbry (1927: 171; plt. 11, fig. 4c) reported that the dart of *H. buffoniana* (Pfeiffer) was about 5 mm long, circular in cross section, slightly curved, hollow, and with thin walls. It would be consistent for the papillae found in *H. fullingtoni* to secrete darts of this type by binding the loose calcium granules onto their surfaces.

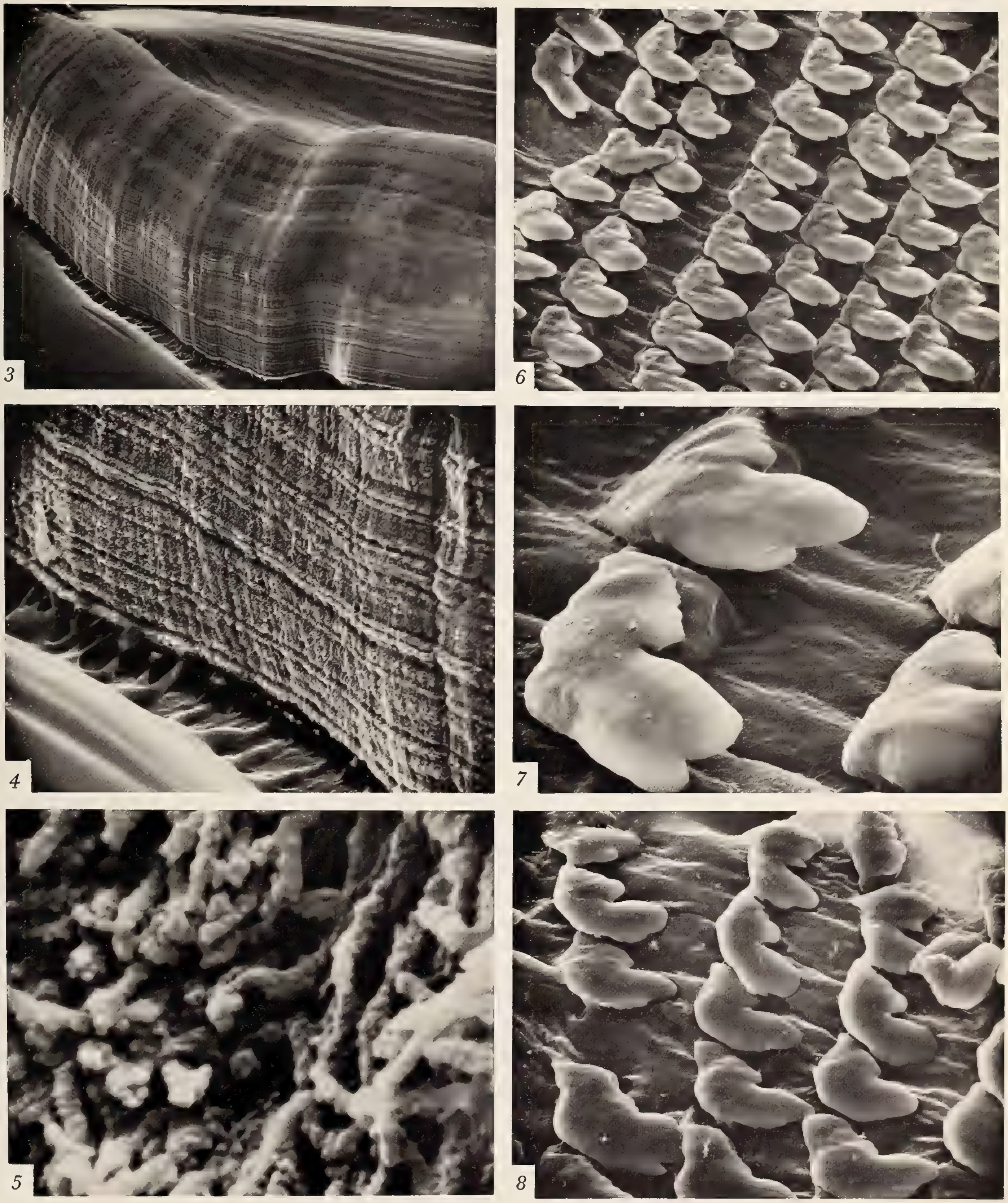
The jaw (Figure *3*) has quite weak ribs compared with the normal pattern for *Humboldtiana* (Pilsbry, 1927: 167; fig. 1, a, b and 1939: 396; fig. 265). It is most similar to the type specimen of *H. texana*. More detailed views (Figures *4, 5*) show that the jaw is composed of multiple horizontally deposited layers, which in turn are composed of finely intertwined fibers. Since another jaw of *H. texana* figured by Pilsbry was very heavily ribbed, the significance of the weak ribbing is uncertain.

Radular teeth (Figures *6 - 14*) consist of 20 laterals and 29 marginals on each side of the relatively diminutive central tooth (Figure *10*). Latter short and unicuspid, with basal plate twice length of cusp. Anterior margin sinuated,

Explanation of Figures *3* to *8*

Humboldtiana fullingtoni Cheatum, 1972

Paratype. FMNH 170054: Figure *3*: right half of jaw at 73 ×; Figure *4*: detail of jaw showing zonation at 375 ×; Figure *5*: fibers that compose jaw at 1 415 ×; Figure *6*: mid-marginal teeth on the radula at 400 ×; Figure *7*: two mid-marginal teeth at 1 675 ×; Figure *8*: outermost marginal teeth at 800 ×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a middle and two lateral depressions marking the anterior flare. Basal plate with two strong lateral support ridges terminating in a posterior elevation that provides positive interlock with the anterior flare of next tooth in line. First few laterals (Figures *10, 11*) unicuspid, distinctly larger than central, with two anterior pits, but a central flare rather than a sinuation, and a strong lateral ridge on the outer side of the basal plate (Figure *11*). Later right side laterals (Figure *9*) show a shortened basal plate that slants toward the outside margin and a reduced basal ridge. Despite this reduction, interrow support still is possible. Outer laterals (Figure *12*) the basal plate considerably shortened, the supporting ridge reduced to a nub, the lateral pits on the anterior flare greatly reduced in prominence, and the beginnings of an ectoconal protrusion. Whereas the early and mid-laterals have the basal plate distinctly longer than the cusp, by the outer laterals the situation is reversed. Marginals are marked by the addition of a prominent ectocone (Figure *6*) that becomes weakly split (Figure *7*) on mid-marginals. A weak (Figure *6*) to strong (Figure *13*) endocone developed in the mid-marginal range, becoming reduced and/or weakly split (Figure *8*) on outer marginals. Outermost marginals (Figure *8*) frequently distorted, mesocone reduced, ectocone enlarged and split. Figure *13* shows an unusual abnormality, in that two adjacent early marginal teeth are fused at the lower anterior margin.

Worn lateral teeth (Figure *14*) show a combination of broken off cusps and gradual abrasion in the form of striations on the tips.

In form and number, the teeth of *Humboldtiana fullingtoni* are most similar to those of *H. buffoniana* (Pfeiffer) as figured by Pilsbry (1927:169; fig. 2). The latter species is reported as having 28 laterals and 21 marginals, an insignificant difference from the numbers reported above for *H. fullingtoni.*

PATTERNS of VARIATION in *Humboldtiana*

Since the location and identity of the specimens dissected as *Humboldtiana humboldtiana* (Pfeiffer) by Fischer (1899) are unknown, this species is omitted from Table I. Data on mean and range of adult shell diameter and whorl count (based either on published measurements or on specimens examined during this study), penis length, the relative distance between the dart sacs and mucus glands, and the relative length of the free vagina are summarized. The species are ordered from highest to lowest mean whorl count. Species known only from shells are omitted.

While species identification statements have focused primarily on details of shell granulation, color, and banding patterns, inspection of the shell diameter and whorl count data shows that not only are there highly significant differences in diameter and a rather extensive (one whorl) range in mean whorl count, but that whorl count and diameter are not correlated. Actual dwarfing or size increase rather than simple change in whorl count is involved. Mucus glands are scored as short if their distance above the dart sac tip is less than the actual length of the dart sacs, medium if it is about equal, and long if the distance is greater. Length of the free vaginal area, the distance from atrial junction to base of dart sacs, is short if less than length of dart sacs, medium if less than twice the length of dart sacs, and long if more than twice the dart sac length. The length of the penis is taken from literature records and measured as the distance from penial retractor insertion to atrium.

Variation in these features is essentially random and does not correlate with either shell diameter or whorl count. There is a tendency for the free vagina to be proportionately longer than the mucus gland separation. This occurs in six taxa, with the reverse in only two. Nine taxa have the penis 6–9 mm long, four have it 10–12 mm long, and in only one species, *Humboldtiana fasciata,* is there major elongation of the penis. Burch & Thompson (1957; table 1) listed measurements of other parts of the genitalia, summarizing available data. The overall pattern is one of variations that do not show size, geographic, or internally consistent correlations.

Another item of significance concerns the few species in which material from more than one population has been sampled and dissected. *Humboldtiana högeana* (von Martens, 1890), for example, is widely distributed in Chihuahua, *H. durangoensis* Solem, 1954 in Durango and southern Chihuahua, and *H. nuevoleonis* Pilsbry, 1927 is known from several areas in eastern Mexico. Only the latter has been dissected. Other species for which two or more populations have been sampled are *H. fortis* Pilsbry, 1940 and *H. texana.* The genitalia of the *H. fortis* populations (Pilsbry, 1948: 194; fig. 4) show a medium to very long free vaginal area, some difference in mucus gland position, distinct differences in the point at which the spermatheca inserts, and rather differently shaped penes. *H. nuevoleonis* examples (Pilsbry, 1948; 191; fig. 3) differ in mucus gland position, free vaginal length, epiphallus length, and spermathecal duct length. *H. texana,* in contrast, differs noticeably only in respect to free vaginal length, degree of jaw ribbing, and degree of ectoconal development on the marginal teeth of the radula (Pilsbry, 1927: figs. 1, *a*, *b*, 8, 9).

The above differences between populations are of the same order of magnitude as differences used to establish species. This raises questions as to the adequacy of species

criteria used to date, but does not negate the criteria. In no case have two or more species of *Humboldtiana* been collected together. All of the known populations are allopatric. Many are highly restricted in their distribution. Probably they are isolated relicts of formerly widely distributed taxa. The drastic differences in shell size and mean whorl count (Table 1) indicate that experiments in altering the length of organs in the pallial and terminal genitalia have been necessary as the visceral hump was shortened or elongated. This would inevitably alter the spacing and proportions of the genital organs. The relatively conservative penis length suggests stabilizing selection. Probably the extant *Humboldtiana* have not had sympatric congeners that they must recognize as "non-like" snails. In the absence of disruptive selection for species recognition features in the penis, a stable penial size pattern is normal. There are major changes in verge size and pilaster patterns between species. This may be a random "genetic drift" effect.

If the genitalia thus vary as much between populations of what competent systematists consider to be single species, as they do between species, can they be used to delineate species? Presently available data does not permit a precise and complete answer, but a tentative answer and suggestions as to needed investigations are possible. When there are major changes in penial structure, such as the differences between the various species described by Pilsbry (1948) and Burch & Thompson (1957), then there should be no hesitation in giving species recognition. Dissections need to be made of many specimens from the same population in order to determine the extent and pattern of intrapopulational variation. This should then be extended to comparing material from different populations of what probably are the same species. Only when this necessary baseline data is available can we hope to evaluate the significance of observed minor variations in genital proportions and positions.

Finally, brief mention should be made of the unique structures found in *Humboldtiana*. The mucus glands are highly unusual, both in being located far above the dart sac openings, but also in apparently being formed by splitting of the vaginal pilasters accompanied by moderate outpocketing. The dart sacs themselves contain a papilla that secretes a hollow dart, possibly quite different in structure from that found in other helminthoglyptids. The nature of the "apical cavity of the penis" also needs further investigation. In *H. fullingtoni* there was no membrane separating the epiphallus from the verge, and the latter is as wide as the penis apex. In such taxa as *H. fortis* Pilsbry (1948: 190; fig. 2, a; plt. 14, fig. 1) the verge is a minute structure and the epiphallus widens significantly just above the penis. The "star-like" pattern shown in this species probably represents the internal, membrane covered ridges of *H. fullingtoni* shifted to a nearly horizontal, apical position and correlating with size reduction of the verge. The cavity shown for *H. nuevoleonis* (Pilsbry, 1948: 191; fig. 3, b) is perhaps intermediate in prominence, reflecting the slightly larger verge of that species. Species with long verges, such as *H. fasciata* and *H. striata* (see Burch & Thompson, 1957, plt. V, A–C) are reported as having a "vestige of upper chamber." Further study is needed to see if these taxa agree with *H. fullingtoni* in having the corrugations from the epiphallus continue to the verge tip. If this is indeed the case, then the "apical cavity of the penis" is not a discrete structure, but rather a variation in the anterior end of the epiphallus.

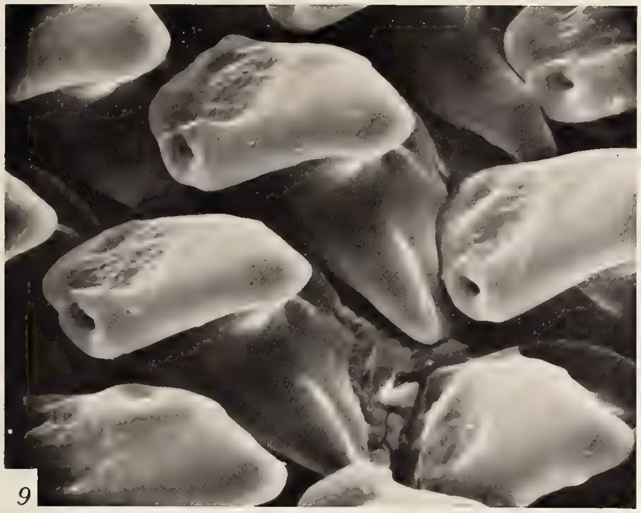
SUMMARY

The pallial and genital anatomy, radular teeth and jaw structure of *Humboldtiana fullingtoni* Cheatum, 1972 are illustrated and compared with previously dissected species. The patterns of genital variation in *Humboldtiana* are shown to be non-correlated, often differing as much between populations of one species as between described species. Penial structures appear more conservative and there are significant differences in verge size and shape that probably are indicative of species differences. Until the range of intrapopulation variation is established by dissecting many individuals from single populations and then comparing variability in several populations, the

Explanation of Figures *9* to *14*

Humboldtiana fullingtoni Cheatum, 1972

Paratype. FMNH 170054: Figure *9*: late lateral teeth at 925 ×; Figure *10*: central and first lateral teeth at 875 ×; Figure *11*: middle part of radula at 435 ×; Figure *12*: outer lateral teeth at 860 ×; Figure *13*: early marginal teeth at 1 830×; Figure *14*: worn lateral teeth at 860 ×.



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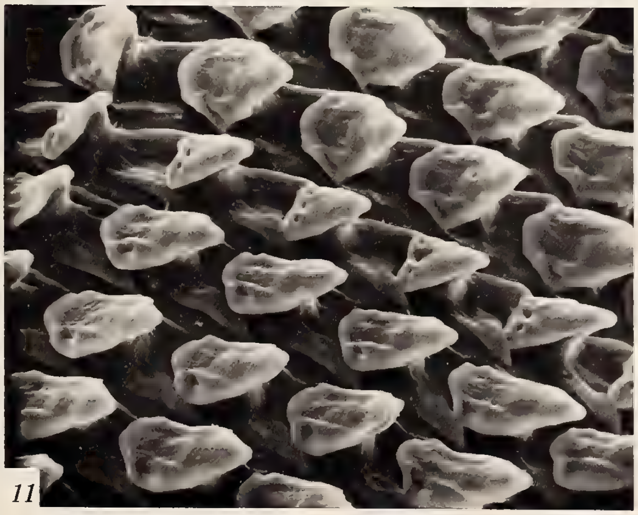

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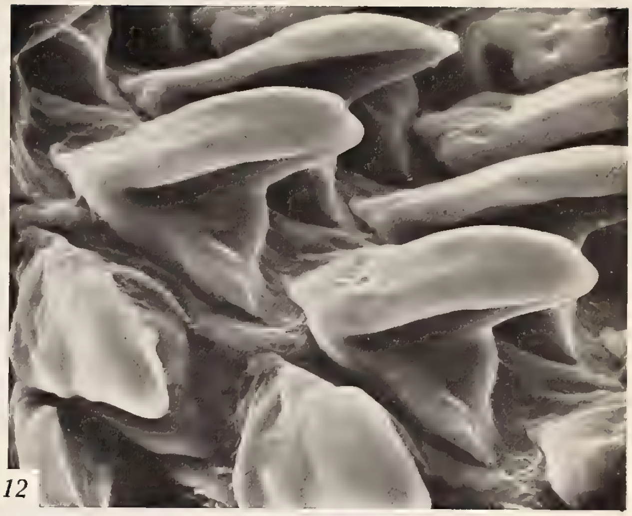

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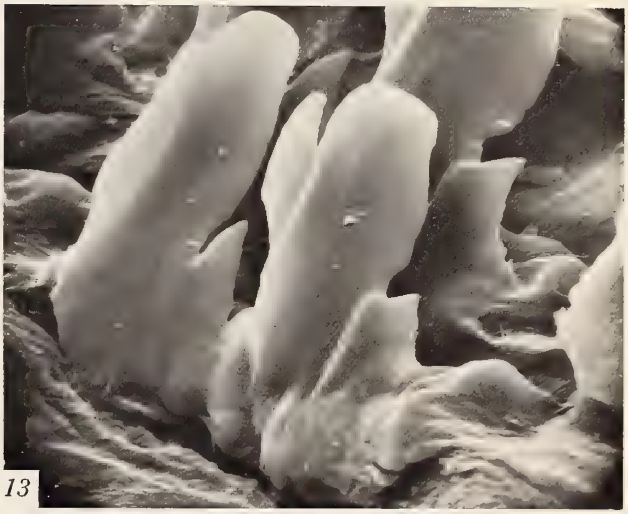

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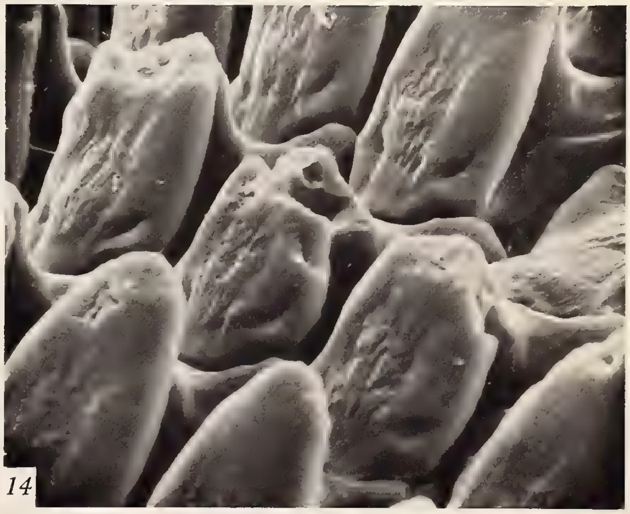

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interpretation of variation will be difficult. The structure and unique features of the mucus gland and dart sacs in *Humboldtiana* are reviewed, and it is suggested that the supposed "apical cavity of the penis" is not a discrete structure, but rather a variation in the anterior end of the epiphallus.

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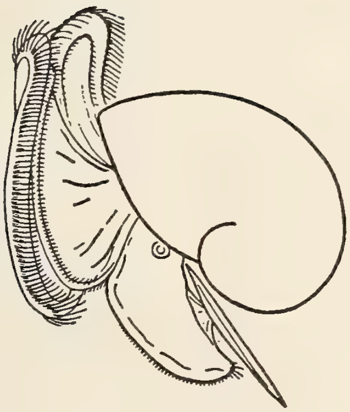

New Occurrences of *Ischnochiton retiporosus* Carpenter, 1864 in the Eastern Pacific Ocean

BY

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The chiton fauna of the continental slope and rise is not well known since samples are not often taken, and thus information on the geographic range, intraspecific variation, and ecology of most deeper water species is sparse. Dredging by Scripps Institution of Oceanography vessels along the western coast of North America has provided several specimens of *Ischnochiton retiporosus* Carpenter, 1864 that suggest that this species is common as far south as the southern tip of Baja California, a considerable extension of its known range. New locations yielding specimens of *I. retiporosus* are:

1. 32°32′54″ N; 117°21′36″ W	137 m	6 specimens
2. 27°01′00″ N; 114°21′06″ W	202 m	1 specimen
3. 26°17′42″ N; 113°46′12″ W	312 m	8 specimens
4. 24°01′00″ N; 111°28′36″ W	453 m	1 specimen
5. 23°45′00″ N; 111°55′12″ W	423 m	1 specimen

Specimens from location 1 (16 km southwest of San Diego, California) were all small (6 mm or less), magenta colored, and immature, with the characteristic valve pustulation poorly developed. The substrate from which they came consisted of shell rubble and small cobbles strewn over a sandy bottom. All of the chitons were attached to old, worn venerid shells; none were found on the rocks. The fact that all 6 specimens were brought up in one dredge-haul suggests that *Ischnochiton retiporosus* is abundant at this depth in this area.

The 8 specimens from location 3 also came from a shell and small rock habitat, and these chitons ranged in size from 5 to 12 mm. It is interesting that all of them (as well as those from locations 4 and 5) had substantial amounts of white coloration on valves and girdle; some being entirely white except for parts of one or two valves which retained the magenta to brown-yellow shades characteristic of specimens from shallower depths. One specimen was dissected; the gut was found to contain much organic matter and rather little (about 25%) sand. The main organic constituents, present in about equal proportions, were benthonic foraminifera of several different kinds and sponge spicules. There were also lesser amounts of radiolarian test fragments, algal detritus, and unidentifiable organic debris. It would appear, as would be expected of a chiton at this depth, that detritus and small, sedentary animals make up the food supply.

The northern limit of *Ischnochiton retiporosus* is in southern Alaska, where it occurs at 27 to 92 m (Berry, 1917). It is present at 147 m off Monterey, California (Smith & Gordon, 1948), and is occasionally taken at depths of 55 to 185 m in Santa Monica Bay, California (Carlisle, 1969). The specimens from locations 4 and 5, besides extending the range of this species to the southern end of Baja California, are from considerably greater depths than have been previously recorded. *Ischnochiton retiporosus* appears to undergo the familiar phenomenon of southern submergence, for its depth in the southern part of its range is about 5 times the typical northern depth. The new locations reported here demonstrate that *I. retiporosus* is one of the widest ranging chitons in the eastern Pacific Ocean. This wide range is probably related to its relatively deep-water habitat.

All specimens reported here are in the Scripps Institution of Oceanography Invertebrate Collections or in the author's personal collection.

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On the Absence of Cuttlefish in the Western Atlantic

BY

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THE QUESTION CONTINUALLY creeps into the cephalopod literature as to whether representatives of the Old World cuttlefish family Sepiidae occur in the Western Atlantic Ocean. Despite repeated statements by cephalopod specialists that they are absent in the New World, various authors continue to assert or intimate that they do indeed inhabit American waters. The latest attempt to "prove" the existence of *Sepia* in the Americas (HARRY & SNIDER, 1969) is so specious, but apparently documented, that an answer is required to lay this new appearance.

It should first be noted that representatives of the genus *Sepia* are very common and numerous in the waters of the Old World. They occur from Scandinavia (but not Iceland or Greenland) throughout European seas (except the Baltic and the Black Seas), along the West African coast to the Cape of Good Hope and throughout the Indian Ocean to Australia and the East Indies. In the Pacific they occur from Japan southward to Australia. They do not extend to New Zealand nor eastward into Oceania. Thus no sepiids occur over most of the Pacific Ocean. They are absent from both coasts of the Americas. Ecologically they occur from along the continental slope inshore over the continental shelf to the shallow waters of bays, harbors and open beaches.

Contrary to the impression given by HARRY & SNIDER (1969: 91), most sepiids are not secretive and are easily caught by the use of lures, spears, baits, traps and commercial trawling gear. The latter means is particularly effective and trawlers annually produce thousands of tons of *Sepia* in such diverse waters as the Saharan Bank between the Canaries and the African coast (~20 000 metric tons) (VOSS, 1973) or the continental shelf around Hong Kong (1 000 metric tons) (VOSS & WILLIAMSON, 1972). Several tons are sometimes taken in a single trawl haul. In West African waters the writer, working aboard the R/V *John Elliott Pillsbury* of the University of Miami and using standard 41-ft. (12.3 m) Gulf of Mexico shrimp trawls, took numerous specimens of all 5 species of West African Sepiidae (VOSS, in press). Several thousand tows with similar gear on similar bottom from French Guiana to Yucatan, the Antilles to Miami have taken not one specimen!

In contrast to the shells of most other mollusks, the shell (cuttlebone or sepion) of sepiids is minutely chambered and very light. While clam shells on the bottom are fairly good indicators of the former presence in the vicinity of a living clam, the shells of sepiids on a beach, unless in large quantities, cannot be taken as evidence of the former presence of a living animal. Indeed, the animal from whence the sepion originated may have lived in waters thousands of miles distant. Ships working in the area off the Gulf of Guinea regularly encounter windrows of cuttlebones floating on the surface, often many hundreds of miles at sea. The shells are clean, usually uninjured, and in large numbers. They are easily identifiable. These cuttlebones lie directly within the origins of both the North and South Atlantic Equatorial Currents which flow to the westward, later to bathe the beaches of the Caribbean and North and South America. It is natural that these currents should and do transport cuttlebones to American waters.

The writer has specialized in the study of the cephalopods for about 20 years. During this period several dozen cuttlebones have been sent in for identification, taken from various localities in the Americas, and each one, when the condition of the shell permitted specific identification, has been found to have come from a known European or African species. No specimens, still retaining characters of specific value, have been unidentifiable, unusual, or aberrant. During the month of March, 1972, 2 cuttlebones were obtained, one from Boynton Beach, Florida, by Mr. Thomas McGinty and one from Chub Cay, Bahamas, by Dr. Donald de Sylva. Both were sent to the writer for identification and proved to be shells of *Sepia officinalis hierredda* Rang, 1837, a common West African species.

The major reason why members of this family have not been able to become established in the Americas is because of the wide extent of deep ocean that they would have to

[1] Contribution No. 1721 from the University of Miami, Rosenstiel School of Marine and Atmospheric Science. This work was supported by National Science Foundation Grant GB-24994X.

cross. *Sepia* are coastal animals living on or near the bottom. While various authors have referred to their seasonal occurrence in deep water, the reference to deep water is used in a comparative sense and refers to the outer continental shelf and continental slope, not to the deep ocean. As a result, adult *Sepia* have been cut off from the Americas by an oceanic deep water barrier.

Similarly, in their early stages the young of the Sepiidae are not planktonic. Sepiid eggs are large, furnished with large supplies of yolk, and the young hatch out and immediately take up a benthic existence. Thus unlike some invertebrates and fishes, the young are not transported long distances as members of the temporary plankton. In other words, both as newly hatched young and as adults, the tropical Atlantic and Eastern Pacific have served as an effectual barrier to the transoceanic migration of the sepiids.

How then has the idea persisted that sepiids have lived or do live in American waters? One reason is the widespread occurrence of cuttlebones on American beaches. Unfortunately (or perhaps fortunately), few of the records have been published as the bones are collected purely as curiosities. As a result, reports are spotty. Harry & Snider seemed to think that some special interest must be attached to the fact that there are no records of cuttlebones from the island of Puerto Rico. Looking at this from a different point of view, we can see that lack of records from particular areas are more artifacts of collecting effort and efficiency than proof that sepiids do not exist in those particular waters. Numerous species of cephalopods are now known to be generally distributed throughout the Gulf of Mexico and Caribbean Sea, yet they have only been reported in the literature from a few widely separated places.

The other so-called evidence for the existence of *Sepia* in the Western Atlantic is based upon a few early popular reports of *Sepia* in tropical Atlantic waters and two apparent records in the scientific literature. Both of these latter are referred to by Harry & Snider: d'Orbigny (1841) and Oliveira (1940).

I cannot vouch for the identity of d'Orbigny's specimen. It was originally labeled *Sepia orbignyana* and according to his account (1841) was from the island of Martinique. As it did not agree with the true *S. orbignyana* which comes from Europe and Africa, he named it *Sepia antillarum*. However, the cuttlebone was missing and the remaining fleshy parts of the animal were in such poor condition that **no specific characters are given.** In his great monograph of the cephalopods he (d'Orbigny, 1848: 290) placed *S. antillarum* among the Uncertain Species with the statement that he only had a single specimen and that it was in such poor condition that it was unable to be characterized. I have searched the collections of the Paris Museum for all specimens originating in the Americas; this specimen has not come to light. Adam & Rees (1966) in their great monographic treatment of the family Sepiidae retain the name as a valid one in their list of species and varieties of Sepiidae but with the comment that it is a "doubtful species" (p. 149). This opinion of the record is clearly given in an earlier statement (p. 145) "As to geographical distribution, it is first of all noteworthy that no Sepiidae have ever been found on the coasts of the American continent or on those of New Zealand, except as stranded cuttlebones."

It is my opinion that either d'Orbigny misidentified the poor remains being misled by the previous identification and supposing that there had originally been a cuttlebone since removed, or that the location was in error, a not infrequent occurrence in early museum labels. Remember that *Cassis madagascariensis* was so named because the label said Madagascar whereas the living specimens occur in Florida and the Caribbean!

The other so-called positive proof of living *Sepia* in the Americas is the description of *Sepia officinalis jurujubai* by Oliveira (1940). This was an unfortunate paper since the description was based clearly upon a specimen of the loliginid squid *Sepioteuthis sepioidea* Blainville, 1823, a common reef squid of the tropical Atlantic; it seldom occurs as far south as this specimen did. There is no doubt about the mistake; the cuttlebone was not illustrated, as pointed out by Harry & Snider, for the very good reason that there was none. Dr. W. Adam (personal communication) has drawn my attention to the fact that Adam & Rees (*op. cit.*: 151) synonymized *jurujubai* under *Sepioteuthis sepioidea*. It is very possible that d'Orbigny's *Sepia antillarum* was a poorly preserved specimen of the same species. The specimens referred to by Brown (1756) also were most probably *Sepioteuthis*. The generic name *Sepia* was widely and indiscriminately used in the popular literature for various genera of squid even as late as the middle 1800s.

Sepioteuthis sepioidea is a true loliginid that strongly resembles *Sepia*; the body is oval, the fins are marginal the length of the mantle, the head is large with prominent eyes and the arms and tentacles are stout. It also has the habit of hovering over coral and grass and changing colors rapidly as do *Sepia*. The name itself means the "Cuttlefish squid that looks like a cuttlefish." The only major thing missing is a cuttlebone (!); it has a typical loliginid gladius of chitin. It is this animal that has for years been referred to as *Sepia* in popular and semipopular natural history accounts. With occurrence of cuttlebones washed up on the beach the existence of cuttlefish in American waters seemed confirmed.

In summation I can say that despite thousands of otter trawl hauls by such vessels as the R/V *Oregon, Pillsbury, Eastward, Alaminos,* and others, the studies carried out in shrimp investigations from Brazil to Miami, and literally thousands of observations by swimmers, snorkel and SCUBA divers from the surface to in excess of 60 m and investigations by research submersibles, not a single living or dead whole *Sepia* has ever been seen in the Western Atlantic.

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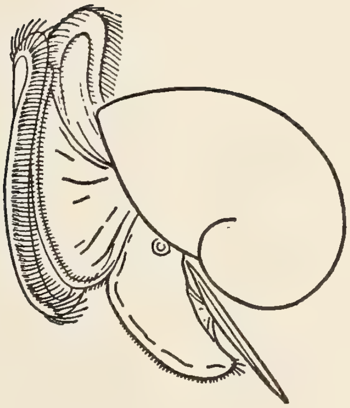

A Phenology of the Smaller Dendronotacean, Arminacean and Aeolidacean Nudibranchs at Asilomar State Beach Over a Twenty-Seven Month Period

BY

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(1 Text figure)

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INTRODUCTION AND METHODS

LONG TERM STUDIES on the populations of nudibranch mollusks are practically non-existent. This is probably due, at least in part, to the difficulty in finding large populations (POTTS, 1970) and to a prevailing feeling that these animals are only transitory members of the communities in which they are found. However, as THOMPSON (1964) and MILLER (1962) pointed out, there are ecologically two groups of nudibranchs, those with short life spans feeding on irregularly abundant prey and characterized by rapid reproduction, and transitory appearances; and those with annual or longer life spans feeding on regularly abundant prey and characterized by annual reproduction and more stable populations. The former species group would fall into what MACARTHUR (1960) has termed opportunistic species and the latter into his equilibrium species. For the past four years I have been conducting a long-term study of the abundance, diversity and temporal variation in an assemblage of intertidal nudibranchs which fall into the equilibrium ecological group. This study has been conducted at Asilomar State Beach, Pacific Grove, California (long. 121°56′24″W; lat. 36°37′36″N). Ancillary to this major study I have also been recording the presence and abundance of the opportunistic species which in this case means most of the eolid, dendronotacean and arminacean nudibranchs. It is the purpose of this paper to report the changes and seasonality observed in the later groups over 27 months.

The study area is an irregular area about 50 meters by 50 meters lying in the low intertidal zone (zone 4 of RICKETTS & CALVIN, 1968) and is uncovered by tides falling to –0.5 or lower. It consists of dissected granitic rock outcroppings and ridges with several large tidepools. The dominant algae are *Egregia menziesii, Macrocystis integrifolia,* and several species of *Gigartina.*

Since the results reported here were obtained as an ancillary part of the study on the equilibrium group of nudibranchs, the methods were the same as employed in that study. The method was simple. Once each month, save September which had no tides below –0.5, on a date on which the tide fell below –0.5 ft., three qualified observers would enter the study area, each proceeding to his own specified sub-division. Each would enumerate the numbers of individuals of each species of nudibranch observed in a one hour interval.

Early in the study it became apparent that we could not enumerate quantitatively most of the eolid, arminacean, and dendronotacean nudibranchs. This was due primarily to their small size and often cryptic coloration. I therefore removed them from consideration in my study of nudibranch population ecology, but continued, nonetheless, to enumerate them in hope some useful information could be derived.

RESULTS AND DISCUSSION

The species of eolid, arminacean and dendronotacean nudibranchs observed and the months of occurrence over 27 months are given in Table 1 and graphically in Figure 1. The time period for these data is from April, 1971 through June, 1973. I have also plotted (Figure 1) the numbers of individuals enumerated each month. Although I believe that the numbers of species enumerated represent real trends, I do not suggest that they are adequate quantitative samples of true populations, and hence I have not attempted rigorous statistical treatment.

Table 1

Months of occurrence of 17 smaller nudibranchs at Asilomar State Beach

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Oct	Nov	Dec
Dendronotus frondosus (Ascanius, 1774)				3, 5	3	3	3, 4	3, 4			
Dendronotus subramosus MacFarland, 1966					4		4	3?	3	3	
Precuthona divae Marcus, 1961		4		3		3, 5	3, 4		3, 4	3	
Trinchesia lagunae (O'Donoghue, 1926)		5		3, 4, 5	3, 4, 5	4	3, 4		4	3	3
Coryphella trilineata O'Donoghue, 1921	4	4, 5	4, 5	4, 5	3, 4, 5	3, 4, 5	3, 4	3, 4	3, 4	3	3
Doto amyra Marcus, 1961		4			3, 4, 5	3, 4, 5	3, 4	3		3	3
Catriona alpha (Baba & Hamatani, 1963)				5	5	3, 4					
Hancockia californica MacFarland, 1923						3, 5	3	3, 4	3, 4	3	
Spurilla chromosoma Cockerell & Eliot, 1905							3				
Trinchesia flavovulta (MacFarland, 1966)				4, 5		4, 5		3	4		
Trinchesia albocrusta (MacFarland, 1966)						5	4				
Trinchesia fulgens (MacFarland, 1966)					5	4, 5					
Trinchesia abronia (MacFarland, 1966)							4				
Spurilla oliviae (MacFarland, 1966)				5							
Doto kya Marcus, 1961					5	5					
Eubranchus olivaceus (O'Donoghue, 1921)					5						
Eubranchus rustyus (Marcus, 1961)					4, 5	5					
Total number of species present per month over a 3-year period	1	4	1	7	10	12	9	8	6	6	4

Starting month is April 1971
3=1971 (Jan, Feb, Mar not counted)
4=1972
5=1973

I should point out that there are certain species which I have not considered here. These are mainly the larger and more conspicuous forms which ecologically appear to belong to the equilibrium group and are considered in another paper. These species are: *Hermissenda crassicornis* (Eschscholtz, 1831), *Aeolidia papillosa* (Linnaeus, 1761), *Dendronotus albus* (MacFarland, 1966), *Tritonia festiva* (Stearns, 1873), *Antiopella barbarensis* (Cooper, 1863), and *Phidiana pugnax* Lance, 1962.

Of the 17 smaller species reported here, only *Coryphella trilineata* seems to be present during the whole year (Table 1). Not only is it present most of the time, but it usually is the most abundant as well. It is a predator on hydroids and appears, from my observations, to be very catholic in its diet.

If one considers these small nudibranchs as a group, certain definite trends appear in the data. The most important fact which emerges is that both the number of species and the numbers of individuals of these small nudibranchs go up in late spring and early summer and decline drastically in the fall so that few or no species are present during the winter months. In other words, this group of species is very seasonal in their occurrence and the season is the same in succeeding years (Figure 1). Both the numbers of species and numbers of individuals are highly correlated with season (Spearman rank $r_s = 0.99$; $P \ll 0.01$).

Although the food is not known for many of the species, reference to the literature reveals that species in the same genus in other parts of the world feed on hydroids (Thompson, 1964; Miller, 1961; Swennen, 1961). The absence, then,of these species in winter may be due to the absence of suitable hydroid species. That *Coryphella trilineata* is able to persist may be due to the fact that it is capable of switching to whatever hydroid is available and also suggests that the other species are more specialized in their diet. That this latter situation may in fact be the case can be substantiated by noting that *Precuthona divae* prefers to feed on *Hydractinia* sp. and *Eubranchus olivaceus* on *Obelia commisuralis* (Waters, unpublished).

I have not noted the species of hydroids present in the study area during various seasons, but I have noted that

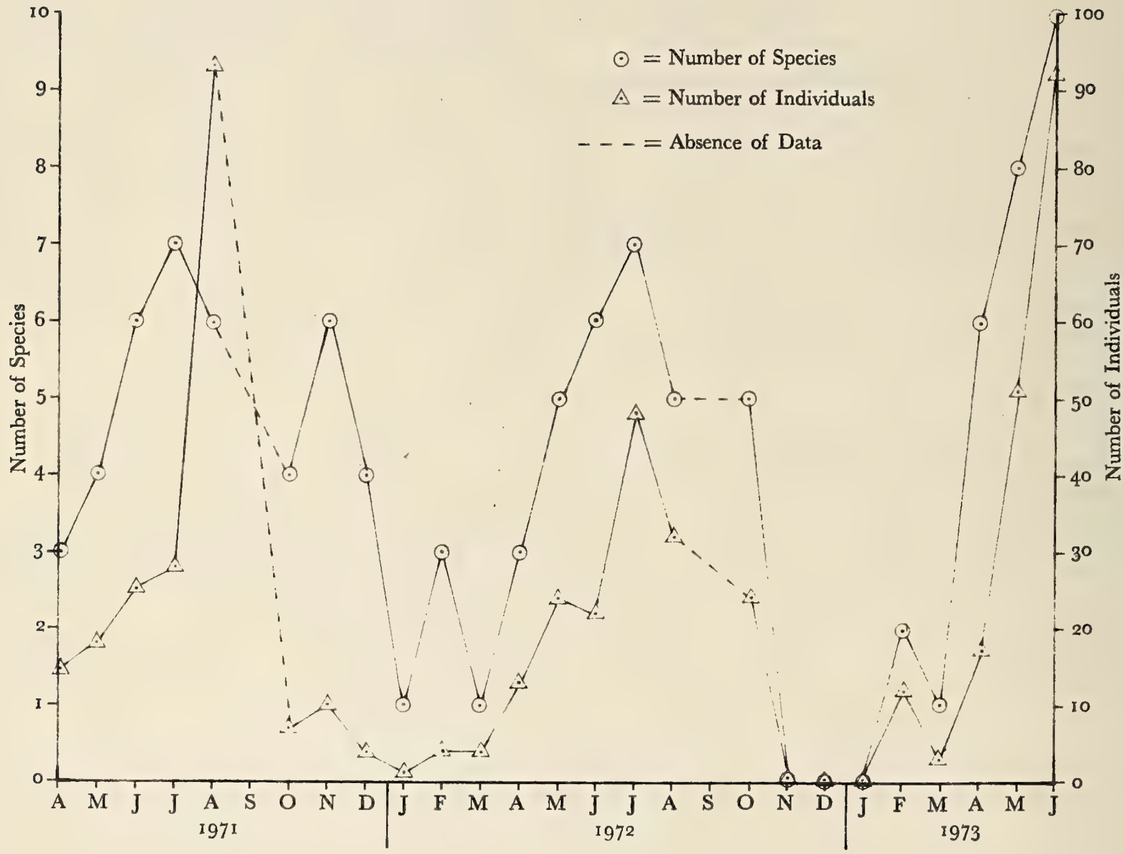

Figure 1

Changes in the number of species and numbers of individuals of eolid, arminacean, and dendronotacean nudibranchs at Asilomar State Beach over a 27 month period

at least some hydroid material is present in every month. Hence it would appear that were all the species to some extent generalists, they should not show the marked seasonality that they do.

It may also be argued that the reason for the lack of these small species in winter is simply a matter of weather. This is the storm season and even at low tide the study area is often flooded by surges from the heavy large waves. Under these conditions it would be easy to overlook these small nudibranchs or, alternatively, they are not out in the tidepools but hiding in the rocks or algae. I cannot prove that this is not the situation, but I do know that periods of very calm, fine weather have often occurred during the winter when we have been counting and still these species were not present. I do not think that we would have missed them had they been there.

Since the time of reappearance of these species seems to be constant, or nearly so, from year to year, it might

also be suggested that this fluctuation in abundance is the result of seasonal migration. That is to say that the species migrate into the intertidal zone in spring and summer from deeper water offshore for the purpose of breeding or feeding, or both. This concept has been discussed by MILLER (1962) who concluded that nudibranch migrations do not occur. After 4 years of observation at Asilomar, I feel certain that migration does not occur in the equilibrium species. In the case of these opportunistic species with their short life spans and small size I find it difficult to believe that they could accomplish the migration necessary to bring them into the intertidal zone, and hence I must agree with Miller.

Thus I conclude that the reoccurring periods of abundance and scarcity on a seasonal basis are real and reflect changes in the conditions necessary for the existence of these species. Though I suggest that the periodicity in the presence of the appropriate food organism is the reason for periodicity in the nudibranchs, other explanations have not been eliminated and should be explored.

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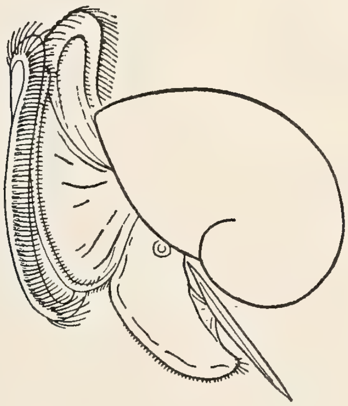

A Late Pleistocene Terrace Faunule from Near La Jolla, California

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(1 Plate)

INTRODUCTION

In the spring of 1970, the senior author while on temporary leave at the Scripps Institution of Oceanography, undertook a study of the raised Pleistocene terraces near La Jolla, California. The purpose of the investigation was to obtain material suitable for radiometrically dating the various terrace deposits.

In the course of reviewing the pertinent literature, reference to a low emergent terrace at Scripps Institution, which has received little notice in the published literature, was found in the unpublished Master's thesis of W. B. Merselis (1962). Merselis described the location and morphology of the terrace and shorecliff but did not record the presence of fossils in the terrace sediment. Because of the accessibility of the site, the clarity of the geological relationships, and the common difficulty elsewhere in locating clearly exposed sites where the ancient shoreline angle can be defined, the site, the fossiliferous terrace sediment, and the enclosed fossils, are herein described.

GEOLOGY of the SITE

As described by Merselis, the raised shoreline angle (the intersection of the shorecliff and wave-cut bench) is 167 m north of the Scripps Pier (Figure *1*); the terrace slopes southward and disappears below the present beach level directly north of the Pier. Conglomerate near the contact between the Ardath Shale and Scripps Formation of Eocene age (Kennedy & Moore, 1971) underlies the Pleistocene terrace deposit. Slickensided vertical fault surfaces, showing strike-slip movement, cut through the conglomerate a few meters south of the shoreline angle in a northwesterly direction, and are probably related to the Rose Canyon fault, which is known to trend offshore in this vicinity (Kennedy & Moore, *op. cit.*). The displacement and relative age of the faults might be determined by locating their intersection offshore with the Miocene Scripps dike dated at 10.9 ± 1.1 million years (Kennedy & Moore, *op. cit.*); the dike trends southwestward offshore from its outcrop, located about 450 m north of the terrace site. The alteration of the Eocene rocks along faults and the resulting differential erosion perhaps served as the agents to create a small promontory, into which small sea caves are developing, at the terrace site (Figure *2*). The faults do not cut the Pleistocene terrace sediment, exposed in the ceilings of the caves and in the present shorecliff. In both types of exposures, metazoan invertebrates are preserved and occur meagerly in the interstices of the coarse terrace sediment.

Merselis (1962) measured the altitude of the raised shoreline angle as 21 feet (6.4 m), and noted that the terrace slopes southward at a relatively steep slope of four degrees. He also noted that the coarse rubble of the terrace sediment diminishes in size from an average of one foot (30 cm) diameter at the shoreline angle to about three inches (8 cm) at a distance of 170 feet (52 m) to the south. Although he recorded the common occurrence of pholad borings in the terrace boulders, he did not note the presence of preserved fossils.

Above a few meters of terrace sediment are more than 10 m of fine-textured alluvial and colluvial sediments, mostly buff to light brown in color (Figure *3*). At inter-

vals through these overlying sediments, reddish-brown zones and charcoal occur. These, a formerly-exposed hearth near the base of the alluvium, and artifact-bearing levels in the upper 2 m, have aroused archaeological interest, through which the cliff has become known as the Scripps site (SELLARDS, 1960), or the SIO Cliff Site (HUBBS et al., 1962). CARTER (1957, p. 241) and other authors have also discussed the archeological aspects of this site.

PALEONTOLOGY

The terrace sediment ranges from boulder gravel to silt and sand, partly cemented by iron oxide. Extraction of the sparse fossil fauna was a difficult and slow process, involving part-time effort over a period of several weeks. Because of the limited time available, only a few specimens were recovered; specimens were frequently broken during recovery from the matrix.

The molluscan taxa, together with ecological notes based largely on FITCH (1953) and McLEAN (1969), are given below.

Mollusca

Gastropoda

1. *Lacuna unifasciata* Carpenter, 1857. Intertidal to sublittoral, on eelgrass, algae. 2 specimens.
2. *Thais emarginata* (Deshayes, 1839). Intertidal, on rocks near mussel beds. 1 specimen, lacking spire.
3. *Tegula* cf. *T. funebralis* (A. Adams, 1855). Intertidal on rocks. 10 + fragments, some of which may represent *T. gallina* (Forbes, 1852), a species commonly associated with *T. funebralis* in the midtidal zone.

Bivalvia

1. *Mytilus* cf. *M. californianus* Conrad, 1837. Upper intertidal zone, on exposed rocks, but also may occur sublittorally (Berry, 1954; Chan, 1973). Numerous fragments.
2. *Ostrea lurida* Carpenter, 1864. Intertidal, in sheltered inlets and bays, attached to hard substrates, common on mudflats. Numerous valves.
3. *Hinnites multirugosus* (Gale, 1928). Low intertidal to sublittoral attached to rocks and other hard substrates in bays and along open coasts. 2 fragments.
4. *Pseudochama exogyra* (Conrad, 1837). Mid-intertidal, along open coasts, rarely in bays or protected coastal waters, attached to rocks or other hard substrates. 2 valves.

In addition to the mollusks, several fragmental echinoid spines, which are referable to *Dendraster* sp. indet., a few echinoid test fragments, and several fragmental plates of barnacles, *Balanus* sp.?, were recovered.

All the identified molluscan taxa are known to be living at the latitude of the terrace site, and these species are common constituents of the modern Californian faunal province. Two major molluscan life associations are apparently represented in the meager collection. An exposed, rocky shore element is characterized by the presence of the *Mytilus, Tegula* and *Thais*. The common occurrence of *Ostrea* suggests that elements associated with this species were present in sheltered inlets or bays along the coast.

DISCUSSION

The environment indicated by the fossil fauna is consistent with what can be deduced of the paleogeography of the site. The site was in an exposed position at the base of a high cliff, rather like the present shore cliff. At the higher level of the terrace, the Scripps dike was not likely exposed by erosion as it is today, and the slight protection from the northwest afforded the present beach, was not likely available then. Nearby to the southeast was an embayment in the coast, now occupied by a low urbanized bench, the probable source of the taxa representing a protected environment.

The age of this raised terrace remains a matter of speculation. The fresh, unaltered, condition of the fossils suggests they are suitable for dating by various means. Radiocarbon dates on charcoal in the overlying alluvium range from about 1 000 years B.P. near the top, through about 3 000 years at a depth of about 1.3 m, 21 500 years at about 4.9 m depth, and > 34 000 years at a depth of about 6.6 m (HUBBS *et al.*, 1962, 1963). The indicated age for the terrace fauna is, therefore, some unknown but substantial age greater than 34 000 years. Any reasonable extrapolation downward of the indicated rates of accumulation of the alluvium indicates an age on the order of 70 000 to 100 000 years at the base. Radiocarbon dating of the fossil shells has not been attempted because of the widely held view that marine shell dates over 30 000 years are not trustworthy. A preliminary attempt to apply amino acid dating has suggested equivalence to the lowest terrace of the Palos Verdes sequence near Los Angeles (P. E. Hare, personal communication). Fossiliferous marine deposits on the lowest Palos Verdes terrace, the Palos Verdes sand, have been dated by the helium:uranium method as 95 000 to 130 000 years (FANALE & SCHAEFFER, 1965) and by the open system uranium-series method as 70 000 to 110 000 years (SZABO & ROSHOLT, 1969). The validity of the latter method has

been questioned by KAUFMANN *et al.*, (1971), and the range of results by the various methods does not inspire confidence.

Remnants of a higher raised terrace, also bearing well-preserved fossil shells, occur 5.6 km north of the Scripps site at Torrey Pines State Park and are considered correlative with the Nestor Terrace (VALENTINE, 1960). Shells from the Torrey Pines terrace, with an altitude of about 20 m, were radiocarbon dated at > 50 000 years (HUBBS *et al.*, 1965). Corals from the Nestor terrace at Point Loma have been assigned a tentative age of 125 000 ± 5 000 years on the basis of the Th^{230}/U^{234} method (KERN, 1973b). Although some workers have considered the Torrey Pines terrace to be of Sangamonian age, HUBBS *et al.*, (1965) have suggested it was formed in the second last interglacial stage, and that lower and younger terrace remnants would probably be found in protected coastal sites. The Scripps terrace is likely in that category.

Marine sediment on other terraces occurring at similar elevations in the San Diego area have been referred to the Bay Point Formation, with an estimated age of 100 000 ± years (KENNEDY & MOORE, 1971). However, in view of strong evidence of Pleistocene faulting and warping, (EUGE *et al.*, 1973; KENNEDY & MOORE, 1971; KERN, 1973a; PETERSON, 1970), correlation on altitude alone is not reliable. Dependable correlation will require actual dating of the various terrace segments, largely by methods still being developed and refined.

ACKNOWLEDGMENTS

Dr. F. P. Shepard originally suggested the terrace study and made facilities at Scripps available to Karrow. A grant for field expenses was provided by Dr. W. B. Pearson, Dean of Science, University of Waterloo. We thank Dr. G. W. Moore, U. S. Geological Survey, San Diego, for his comments on the manuscript and Dr. P. E. Hare, Geophysical Laboratory, Carnegie Institution of Washington, for providing information on samples dated by the amino acid method.

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Explanation of Figures *1* to *3*

Figure *1*: Shoreline angle (almost out of picture above seated man's head) and cemented terrace rubble overlying Eocene sandstone and conglomerate on a small promontory. Scripps Institution in right background.

Figure *2*: View of other (south) side of small promontory. Raised terrace extends from sharp angle at left end of promontory to about 1 m below drainpipe. Background cliff beyond promontory is Eocene sandstone.

Figure *3*: Colluvial and alluvial sediments on the raised terrace, which is barely visible at top of lowest dark zone at left of face. Raised terrace dips below the present beach near the right side of the picture. View of cliff face south of area shown in Figure *2*.

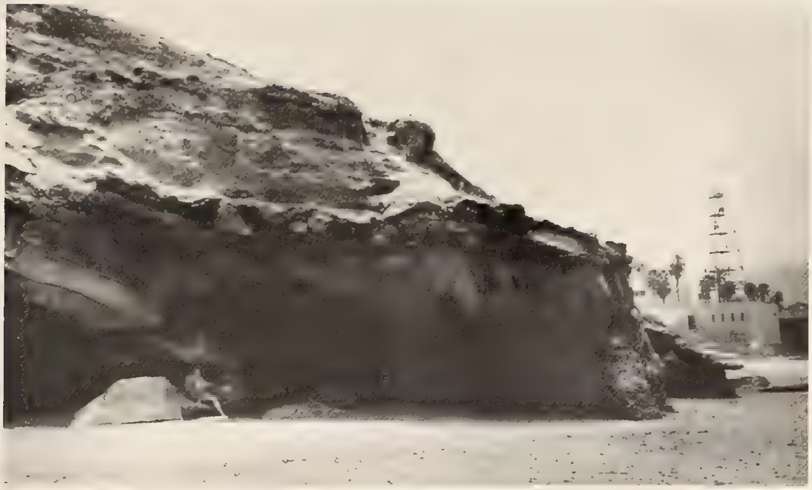

Figure *1*

Figure *2*

Figure *3*

The West American Hipponicidae and the Application of *Malluvium*, *Antisabia*, and *Hipponix* as Generic Names

BY

I. McTAGGART COWAN

(4 Plates)

THE FINDING OF THREE specimens of an unrecognized Hipponicid at Tasu Harbour, Queen Charlotte Islands, British Columbia, has led me to re-examine the representatives of this family described from the Northern Pacific, and to compare these with some other species. MORRISON (1965) described characteristics of the embryonic shell in the Hipponicidae that he believed to be of importance in distinguishing four genera within the conventional genus *Hipponix* Defrance 1819. These were *Antisabia, Sabia, Malluvium,* and *Pilosabia.* The characteristics used were the plane of coiling; the vertical component in the spiral, resulting in either neritoid or amnicoloid form; and the presence or absence of longitudinal surface sculpture.

Specimens in which all details of the larval shell are retained are scarce in collections but I have assembled material representing *Hipponix foliacea* Quoy and Gaimard 1835, *H. lissus* (E. A. Smith, 1894), *H. benthophila* (Dall, 1889); *H. tumens* Carpenter, 1864, *H. grayanus* Menke 1853, *H. serratus* Carpenter, 1857, *H. cranioides* Carpenter, 1864, *H. otohimea* Habe, 1946, *H. antiquatus* (Linnaeus, 1767), *H. panamensis* C. B. Adams, 1852, *Pilosabia pilosa* (Deshayes, 1832) and *Sabia conica* (Schumacher, 1817).

GENERIC DESIGNATIONS

The generic name *Sabia* Reeve, 1842, was based upon the species *H. conica* (Schumacher, 1817) (Figures *3* and *4*). *Hipponix australis* Quoy and Gaimard 1835, is regarded as a synonym of *H. conica* (Cotton 1959), (McPHERSON & GABRIEL 1962).

Sabia conica is an abundant species well represented in collections (Figures *3, 4*). Furthermore it retains its larval shell more frequently than many other species. The larval shell makes slightly less than one revolution. It is much larger than that of frequently sympatric *Hipponix foliacea* and measures about 0.5 mm in diameter. The larval shell is rust red or originally white becoming red by half a whorl, brilliantly glossy on the dorsal surface and is unique in being finely cancellate and in bearing distinct, fine grooves and threads longitudinally on the lower surface only. These grooves average 10 in 0.3 mm before expanding into the post-larval shell. The line of junction is usually distinct. The orientation of the larval shell is variable, frequently about the same as in *H. foliacea* but with a greater tendency to move the transverse axis into a more nearly horizontal plane. The nucleus is variable in form from planospiral to naticoid. Most are planospiral and have the apex broad, blunt, and included within the whorl.

The post-larval shell shows the strong coarse ridging that characterizes the adult shell. These are not extensions of the larval ridges.

The adult shell is fairly uniform in shape, tall, cap-shaped, with the apex close to the posterior margin. Longitudinal ridges fairly regular, broader than the grooves between them, smooth, and with a tendency to bifurcate near exterior margin. I have seen no indication that the foot secretes a basal plate. This species usually occurs attached to the shells of living molluscs.

Pilosabia Iredale, 1929 rests upon the species *Hipponix pilosus* Deshayes, 1832 (Figures *1, 2*). This species has several characteristics distinguishing it from all other Hipponicids. The nucleus is naticoid with a relatively high spiral and the nuclear apex fine and not adpressed to the adult shell. The mature animal secretes a thick basal plate bearing incremental lines. The nucleus consists of almost two complete whorls; ½ to ⅔ the depth of each whorl free; main axis vertical or rotated 45°; entire embryonic shell held separate from adult shell; extended, terminal,

smooth, opaque, white, becoming brownish at flaring base. First increment of adult shell faintly sculptured radially. Adult shell with broad numerous rounded radial ridges, periostracum coarsely bristled. MORRISON (1965) suggests that the name *Patella trigona* Gmelin is an earlier synonym for *H. pilosus*. KEEN (1971) points out that this name is based upon a brief description of a shell from an unknown locality, citing a figure in a nonbinomial work, and rejects the validity of the name. *Hipponix barbata* Sowerby, 1835 appears to be a synonym of *H. pilosus* (Deshayes).

The generic name *Antisabia* Iredale 1937 was applied to *H. foliacea* Quoy and Gaimard, 1835 (Figures *9, 10*). I have examined two dozen specimens in which the details of the larval shell of this species are clearly discernible. Larval shell small (0.13–0.15 mm in diameter), white, translucent, glossy, completely smooth, and naticoid in form; transverse axis usually approximately vertical but inclined dorsally toward the main axis of the shell. Apex of larval shell fine, delicate, and distinct. The post-larval shell, in sharp contrast, bears distinct longitudinal striae. Morrison's statement that the nuclear shell of this species is prominently spirally ridged and neritoid in shape is not borne out by the material I have seen. Perhaps his specimens had become mixed during museum storage.

Malluvium Melvill, 1906 was based upon the species *Hipponix lissus* (E. A. Smith, 1894). This species has a smooth larval shell of about 1½ globose whorls, neritoid in form. Adult shell without sculpture except for incomplete growth lines. The foot secretes a basal plate. MELVILL, 1906 refers *H. benthophila* (Dall, 1889) to the subgenus *Malluvium*. My study confirms *H. benthophila* as having no sculpture on the larval or adult shell (Figures *11, 12*), and in secreting a basal plate. It is unique, however, in the form and position of the larval shell. *Hipponix otohimea* Habe,1946 (Figures *7, 8*) and *H. lissus* (Figures *5, 6*) are similar in details of larval shell but there is no information upon whether or not *H. otohimea* secretes a basal plate.

Thus the characteristics provided by the hard parts of the Hipponicid molluscs include those of embryonic shell, decoration of embryonic shell, shape and decoration of adult shell, presence or absence of a basal plate secreted by the foot, and presence or absence of a thick persistent periostracum.

The characteristics of *Pilosabia pilosa* (Deshayes, 1832) seem to me to be sufficiently distinctive to warrant recognizing the species as a separate genus. The species recognized by MORRISON (1967) as *Sabia conica* (Schumacher, 1817) also has a combination of characters of the larval and adult shells that suggest generic distinction. In these decisions I concur with Morrison.

However, he also suggested dividing the remaining species between 2 genera on the basis of the form and decoration of the larval shell. Inasmuch as he included species of differing larval form in each of his proposed genera, the decoration of the larval shell became the sole basis of separation. He proposed elevating the subgeneric name *Malluvium* Melvill, 1907 to generic status to include the species with smooth larval shells. The species with striated larval shell he referred to the genus *Antisabia* Iredale, 1937. I have shown above that both *Malluvium* Melvill, 1907, and *Antisabia* Iredale, 1937, were originally applied to species with no decoration on the larval shell. On the basis of available information, therefore, *Antisabia* must be regarded as a synonym of *Malluvium*.

SYSTEMATIC STATUS of AMERICAN SPECIES

There has been uncertainty as to the status of *H. antiquatus* (Linnaeus, 1767), *H. panamensis* C. B. Adams, 1852, *H. cranioides* Carpenter, 1864, and *H. serratus* Carpenter, 1857. KEEN (1971) refers to the paucity of characters available for use in systematic distinction of the simple shells of Hipponicids and suggests that the common West American species be recognized as specifically distinct from *H. antiquatus* of the Atlantic shores, pending further information.

Explanation of Figures *1* to *6*

Figure *1*: *Pilosabia pilosa*, adult shell
Figure *2*: *Pilosabia pilosa*, larval shell
Figure *3*: *Sabia conica*, adult shell
Figure *4*: *Sabia conica*, larval shell
Figure *5*: *Hipponix lissus*, adult shell
Figure *6*: *Hipponix lissus*, larval shell

Explanation of Figures *7* to *12*

Figure *7*: *Hipponix otohimea*, adult shell
Figure *8*: *Hipponix otohimea*, larval shell
Figure *9*: *Hipponix foliacea*, adult shell
Figure *10*: *Hipponix foliacea*, larval shell
Figure *11*: *Hipponix benthophila*, adult shell
Figure *12*: *Hipponix benthophila*, larval shell


Figure *1*


Figure *2*


Figure *3*

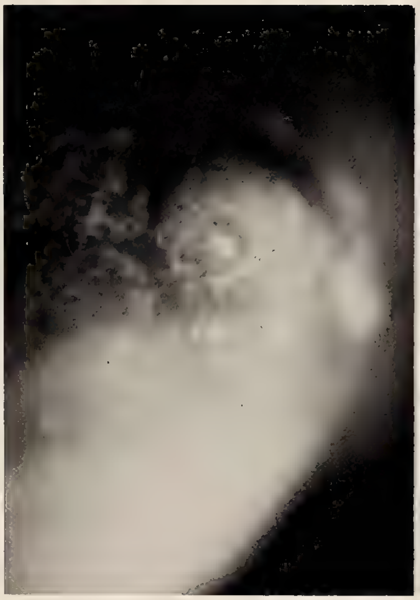
Figure *4*

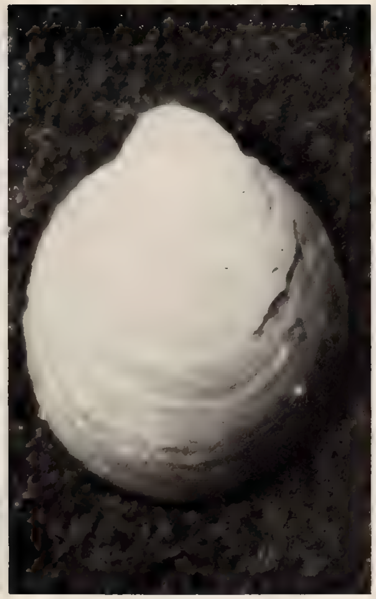
Figure *5*


Figure *6*

Figure *7*

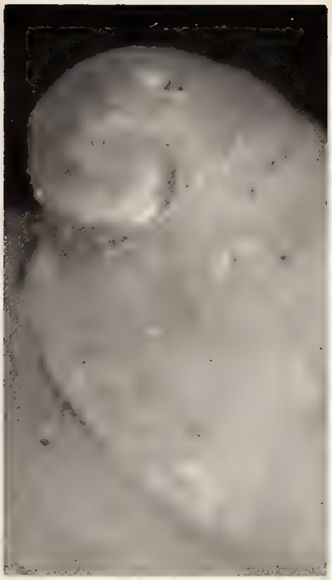

Figure *8*

Figure *9*

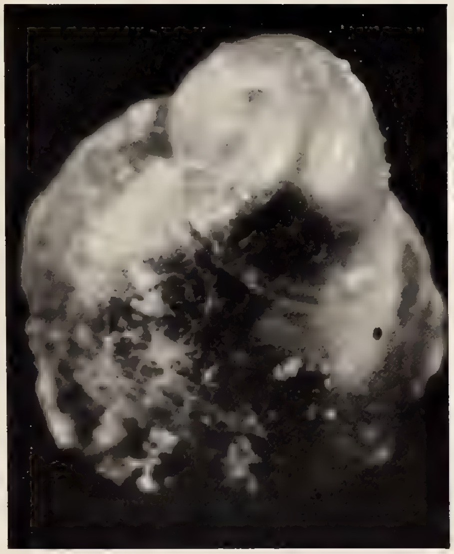

Figure *10*

Figure *11*

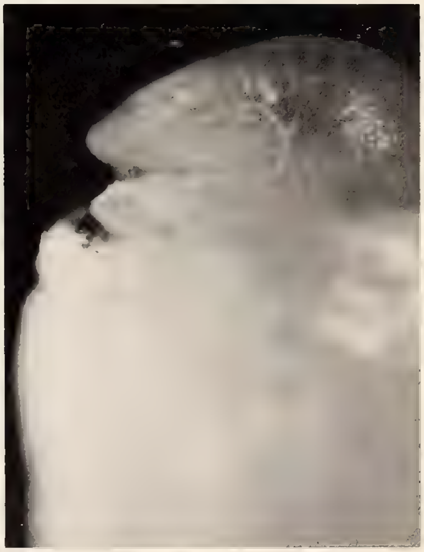

Figure *12*

Specimens bearing the larval shell of these 'species' are very scarce in collections, but I have been able to obtain excellent specimens of *Hipponix cranioides* Carpenter, from Vancouver Island, B.C., and *H. antiquatus* from Guadeloupe, (Phila. Acad. Sci. #3;3830). The larval characteristics of *H. panamensis* C. B. Adams, 1852, remain uncertain.

The specimens now available reveal that the larval shell of *Hipponix antiquatus* is markedly different from that of the West American forms.

Hipponix antiquatus has the most heavily sculptured larval shell of any member of the family yet examined (Figure *22*). It is planospiral, vertical in position, rotated to the right, describes not quite one turn, and is heavily patterned with spiral ridges $10 \pm$ in number and extending even onto the tip of the nucleus. In this it is unique. In most specimens of this species the larval shell is only narrowly attached to the underlying adult shell and extends over its posterior margin.

The first increment to the young adult shell bears clear longitudinal striae that continue onto the older shell but on it are less obvious than the circular sculpture of delicate projecting fimbriae (Figure *21*). Longitudinal striae are not visible on the fimbriae. As the shell matures and encounters abrasion most surface details are lost.

The larval shell of Vancouver Island specimens (*Hipponix cranioides*) is larger than that of *H. antiquatus*, planospiral, horizontal in position and broadly attached to the underlying adult shell. Longitudinal ridges are present all around the shell but are visible with difficulty, and it is not certain whether they are present on the tip of the nucleus (Figure *16*). The longitudinal striae of the post-larval shell are heavier and remain prominent on the relatively unworn adult shell, even extending to the margins of the circular, projecting fimbriae, which in this species are thicker and less prominent than in *H. antiquatus*.

Both species can secrete a heavy basal plate. Both species are highly variable in shape of the adult shell, but many of the West American specimens have the apex subcentral, and in few does it overhang the back margin as it does generally in *Hipponix antiquatus; H. cranioides* and *H. antiquatus* appear to form a species pair separated by the Central American land mass.

I have been unable to find in any existing collections, or in my field work on the Pacific coast of Mexico, a series of larval specimens of *Hipponix* that can be clearly related to the taxon described by Carpenter as *H. panamensis* (Figures *13, 14*). Mature shells allocated to this species reveal few if any constant characters to distinguish them from *H. cranioides*. On the other hand a young shell believed to be of this species (Figures *13, 14*) is clearly different from *H. cranioides* at similar stages, in form and sculpture of both the nucleus and the post-larval shell. Until more unworn specimens are obtained it seems best to recognize *H. panamensis* as a distinct species, rather than to follow Keen (1971) in designating it as the valid name to include *H. cranioides* Carpenter, *H. serratus* Carpenter, and *H. fimbriatus* Bartsch & Rehder, 1939. I include the last two names as synonyms of *H. cranioides*.

Hipponix tumens Carpenter, 1864, is a recognizable species. It is distinctive in the position of the embryonic whorl. This is turned to the right so as to be transverse to the main axis of the shell. Some appear to be rotated almost 180 degrees. The nucleus is also smaller than in the other American species and sunken; it makes about one turn and is only narrowly adherent to the adult shell. The ridges on the embryonic shell are extremely delicate and apparent only under low angle illumination and $25\times$ magnification. They are also more widely spaced than any other seen, about 4 in 0.3 mm in the only specimen showing this feature clearly. They appear as delicate threads applied to the surface of the shell, present over the entire surface of the shell. These threads are continuous with the ridges of the adult shell.

The adult shell is distinctive, being white and bearing a few widely and evenly spaced narrow prominent ridges separated by broad rounded troughs (Figures *17, 18*); the periostracum is "hairy" along the ridges.

The full characteristics of the shells of *Hipponix planatus* Carpenter 1857, and *Hipponix delicatus* Dall 1908, remain to be described. It is better to postpone decisions on their relationships and validity.

The relationship of *H. grayanus* Menke 1853 to the other species remains uncertain. Only four larval shells have been seen and just one of these was unworn. It showed no spiral sculpture (Figures *23, 24*). This species may therefore belong to the genus *Malluvium* if this proves to be a useful and valid taxon.

DISCUSSION

I now return to the question of whether or not the described characteristics of the larval shell constitute adequate grounds for recognizing separate genera. One can indeed separate the species of *Hipponix* on the presence or absence of larval decoration. On this basis *H. lissus, H. benthophila, H. otohimea, H. grayanus,* and *H. foliacea* are undecorated, whereas *H. antiquatus, H. panamensis, H. cranioides, H. serratus* (Figures *19, 20*), and *H. tumens,* as these names are applied today, have longitudinal striae on the nucleus. If one examines the group in which longitudinal striae are present it is possible to discern a wide

spread in the manifestation of the characteristic. In *H. panamensis* and *H. tumens* the striae are extremely delicate and apparently all around the nucleus. In *H. cranioides* they are broad but faint, and all around the nucleus. In *H. antiquatus* the longitutudinal sculpture is of prominent ridges on all exposed parts of the nucleus. Thus there is an unbroken gradient between smooth larval shells and those with fairly distinct striae. Furthermore, segregation on this basis seems to me to ignore other characteristics probably no less important. The presence or absence of decoration does not appear as a trenchant criterion for generic differentiation. Thus, I urge retention of the genus *Hipponix* to include the species with: undecorated larval shells, or, if decorated the sculpture is present on all surfaces of the shell; the nucleus in close contact, ventrally, with the adult shell, frequently fused to it. Detailed study of soft parts anatomy or biochemical characteristics may subsequently indicate more clearly the existence of grounds for recognizing separate subgenera or genera within this group of species.

I doubt that *Malluvium* is useful even as a subgenus. It could include *Hipponix lissus* and *H. otohimea*, two deep water species with basal plates and with undecorated larval and adult shells. *Hipponix benthophila* Dall included along with *H. lissus* in this subgenus by Melvill, has the most distinctive nuclear shell of any of the species studied. It is large, smooth, translucent, strongly flattened laterally to give a keel along the dorsum, and is set at right angles to the sagittal axis of the adult shell. These larval characteristics might justify generic recognition but I doubt that this would be useful at this point in time.

ACKNOWLEDGMENTS

I am much indebted to Dr. J. Rosewater, United States National Museum of Natural History; Dr. Myra Keen, Department of Geology, Stanford University; Dr. James H. McLean, Los Angeles County Museum; Mrs. Morgan C. Rulon, Academy of Natural Sciences, Philadelphia; and the late Dr. Leo G. Hertlein, California Academy of Sciences, for the loan of the specimens. Figure *17* is enlarged from a photograph taken by Dr. J. H. McLean.

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Morrison, Joseph Paul Eldred
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Explanation of Figures *13* to *18*

Figure *13*: *Hipponix panamensis,* adult shell
Figure *14*: *Hipponix panamensis,* larval shell
Figure *15*: *Hipponix cranioides,* adult shell
Figure *16*: *Hipponix cranioides,* larval shell
Figure *17*: *Hipponix tumens,* adult shell
Figure *18*: *Hipponix tumens,* larval shell

Explanation of Figures *19* to *24*

Figure *19*: *Hipponix serratus,* adult shell
Figure *20*: *Hipponix serratus,* larval shell
Figure *21*: *Hipponix antiquatus,* adult shell
Figure *22*: *Hipponix antiquatus,* larval shell
Figure *23*: *Hipponix grayanus,* adult shell
Figure *24*: *Hipponix grayanus,* larval shell

Figure *13*

Figure *14*

Figure *15*

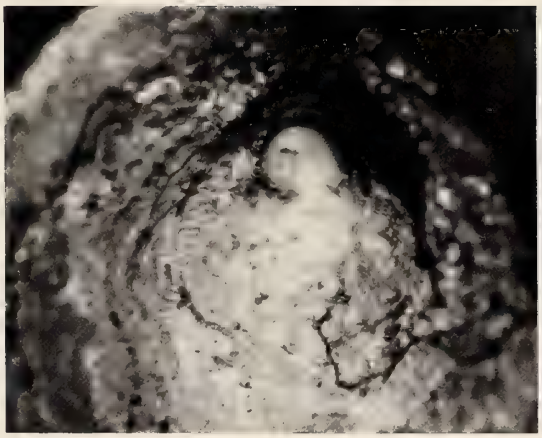

Figure *16*

Figure *17*

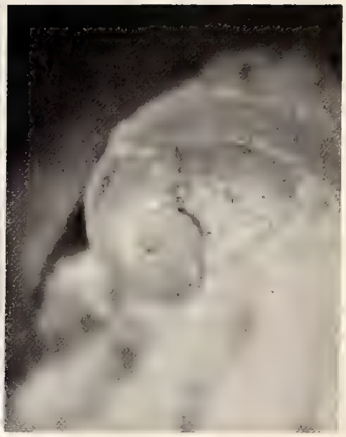

Figure *18*

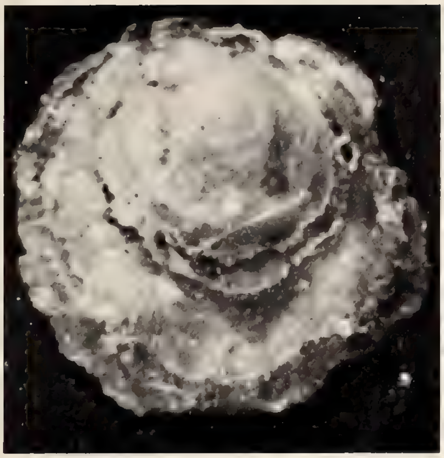

Figure 19

Figure 20

Figure 21

Figure 22

Figure 23

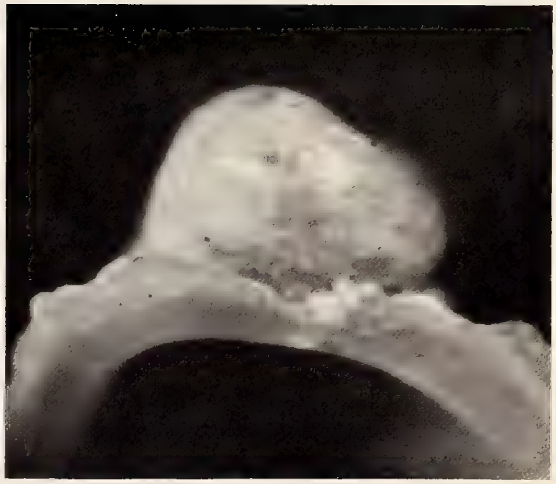

Figure 24

Five New Species of Ovulidae from the Western Pacific

(Mollusca : Gastropoda)

BY

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(1 Plate)

Since the publication of Cate (1973), new interest in the Ovulidae appears to have developed among collectors in various parts of the world, as evidenced by the receipt of numerous parcels of shells from such far-flung areas of the globe as Australia, Cuba, Japan, Philippines, Taiwan, and the west coast of North America. As a result of this activity five additional new ovulid species are proposed herein:

Primovula (Primovula) ***howlandae*** Cate, spec. nov.

(Figure *1*)

Description, holotype: Shell small, solidly formed, roughly diamond-shaped, sub-centrally humped and transversely angled: dorsum closely transversely, incisedly striate over all; adapical terminal projection somewhat pointed, arcuate abapically; base smooth, rhomboidly ovate, narrowing evenly to the front to form a weak terminal ridge; funiculum comparatively large, broad, with several transverse ridges; columella smooth, broad, curving, deepening in front to form a fossula; aperture narrow, evenly curving, broadening only a little abapically, opening to the right posteriorly through peripheral edge of outer lip; outer lip broad, gently sloping adaxially, with numerous teeth evident (on rear half of lip there are 9 boldly developed, coarse denticles which protrude beyond lip edge; teeth on front half of lip are numerous (14), very small, short, though entirely distinct, on inner edge of lip only); dorsum pale grey throughout; base, funiculum, columella, outer lip teeth pale to deep orange-beige; terminal ends and canals bright orange.

Measurements, holotype: L – 6.8; W – 3.7; H – 3.0 mm.

Measurements, paratype: L – 7.7; W – 4.0; H – 3.1 mm. (C 4005)

Measurements, paratype: L – 6.8; W – 3.8; H – 2.9 mm. (C 4017)

Measurements, paratype: L – 6.7; W – 3.6; H – 3.0 mm. (C 4025)

Type Locality: Clairview (Mackay), Queensland, Australia (22°07′ S; 149°32′ E). It is found living at or below tide line on green gorgonian growing in a muddy habitat.

Distribution: Known only from type locality.

Holotype: Australian Museum, Sydney; Register No. C.92105. Paratype: Cate Coll. (C 4005, 4017, 4025).

Discussion: Although this new species, and the recent new species, *Primovula (Primovula) platysia* Cate, 1973, share the same habitat and both species appear similar at first glance (both are light toned in color, and both have bright orange terminal tips); they are, however, decidedly different from one another specifically. *Primovula (P.)* ***howlandae*** spec. nov. differs noticeably by having a smaller shell; by its shorter, broader, more rhomboid form, rather than being long and narrowly ovate; by being more acutely humped dorsally; it has a comparatively larger, more inflated funiculum, with distinct transverse ridges thereon; by having the adapical canal curve dextrally through the periphery of the outer lip; by its more even, parallel apertural opening, flaring restrictedly in front; and by the different combination of shell colors: greyish, rather than white dorsum and a greater distribution of bright orange tinting.

The animals of the two species differ as well: in the animal of *Primovula (Primovula)* ***howlandae,*** the foot is long and narrow, squared at posterior end, barely visible beyond the periphery of the shell—the foot is transparent, with small black spots dispersed generally, and a solid, central black line extending to rear extremity of the nar-

row foot. In *Primovula* (*P.*) *platysia* the foot is also transparent, though very broadly extended beyond the shell's outline, spreading in a large oval form, and covered with fine black spots generally, but with three very large black spots on the foot where it tapers to a point at the rear.

This new ovulid species is named in honor of Mrs. Joan Howland, Mackay, Queensland, Australia, who seems to be the first to recognize this form as new to science.

Cymbovula ***queenslandica*** Cate, spec. nov.

(Figure *2*)

Description, holotype: Shell small, very narrowly elongate (in small, straw colored to off-white specimens the shell is almost translucent); apex narrowly pointed, often distorted by dual dextral and sinistral apertural canal openings; terminals are dorsally thickened due to the influence of a broad callus band that encircles the shell at margin; dorsum rounded sub-centrally because of swollen body whorl, transversely striate over all; base smooth, long, narrow, gently sloping downward adaperturally, angularly constricted abapically, with a large, rudimentary funiculum separating base from apertural canal opening; aperture long, narrow, broadening to the front due to constriction of both base and outer lip, with dual (dextral and sinistral) canal openings posteriorly, with tip of apex drooping slightly between; columella narrow, with a prominently elevated, longitudinal adaxial carina within; outer lip long, very narrow along ventral edge; color dark mulberry-brown overall except that dorsal approach to apex and internal carinal ridge are greyish-white; terminals and wide marginal callus light medium brown.

Measurements, holotype: L – 10.7; W – 3.0; H – 2.5 mm.

Measurements, paratype: L – 10.4; W – 3.3; H – 2.5 mm. (C 3981)

Measurements, paratype: L – 7.6; W – 2.4; H – 1.9 mm. (C 4016)

Measurements, paratype: L – 10.8; W – 3.1; H – 2.5 mm. (C 4026)

Type Locality: Clairview, Queensland, Australia (22°07′ S; 149°32′ E).

Distribution: Known only from type locality.

Holotype: Australian Museum, Sydney: Register No. C.92106. Paratypes: Cate Coll. (C 3981, 4016, 4026).

Discussion: This new species is rather distinct, though it may be compared with *Crenavolva hesperia* Cate, 1973, because of the grotesque appearance of the posterior end (apex) of the shell in both species; however, *C.* ***queenslandica*** has a second sinistral canal opening, as well, on the rear outer lip. The new species differs also by being a longer, narrower, less angled shell; by having less definitive, pronounced labial denticulation; by having a straight, rather than a curving aperture; by having a more pointed, less blunt rear terminal process, and a darker, more vivid combination of shell colors.

The new name is derived from the east Australian state, Queensland, where the species seems to be presently restricted. I am indebted to Mrs. Joan Howland, Slade Point, (Mackay), Queensland, who first noticed these animals, and thought they might be new to science.

Phenacovolva (*Turbovula*) ***greenbergae*** Cate, spec. nov.

(Figure *3*)

Description, holotype: Shell medium in size, somewhat thin, translucent, spindle-shaped, with a central transverse angle [acute in some of the paratypes]; terminals tapering evenly, almost pointed, noticeably reflected and striated; dorsum smooth, glossy, with a weak spiral thickening posteriorly; columella rounded, becoming barely flattened abapically in the fossular area, where the basic darker shell color is visible through the thinned nacre; aperture narrow, long, evenly curving; outer lip thickened, rolled, smooth, shouldered above, and having a bow-like curvature from front to back, due to the apparent reflection of the terminal processes; shell color showing little variation among 8 known specimens, basically whitish-beige overlain by a rich, glossy golden-beige except for a broad, almost obscure transverse band of lighter beige-white; outer

Explanation of Figures *1* to *6*

Figure *1*: *Primovula (Primovula)* ***howlandae*** Cate, spec. nov. × 10
Figure *2*: *Cymbovula* ***queenslandica*** Cate, spec. nov. × 7
Figure *3*: *Phenacovolva (Turbovula)* ***greenbergae*** Cate, spec. nov. × 2
Figure *4*: *Prionovolva* ***nivea*** Cate, spec. nov. × 5½
Figure *5*: *Delonovolva* ***dolabra*** Cate, spec. nov. × 7½
Figure *6*: *Phenacovolva (Turbovula) dancei* Cate, 1973 × 1
Upper figures: Specimen from Taiwan; lower: from the Philippines

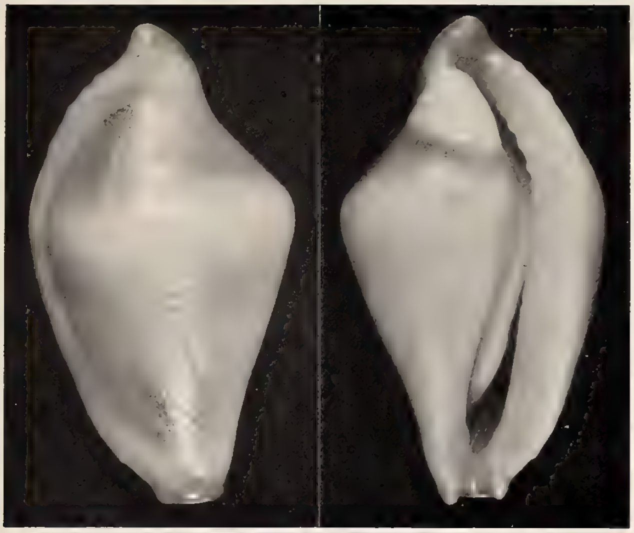

Figure *1*

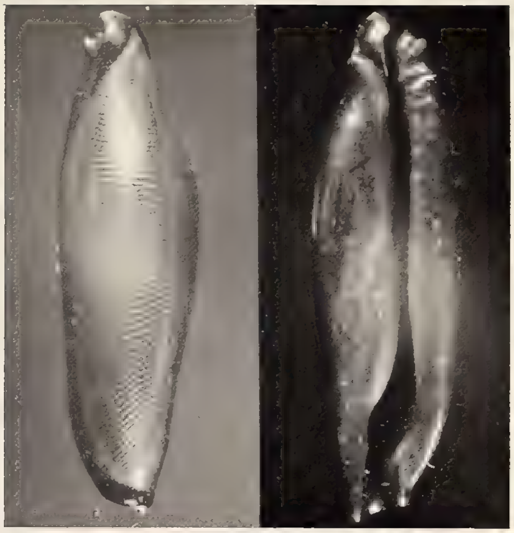

Figure *2*

Figure *3*

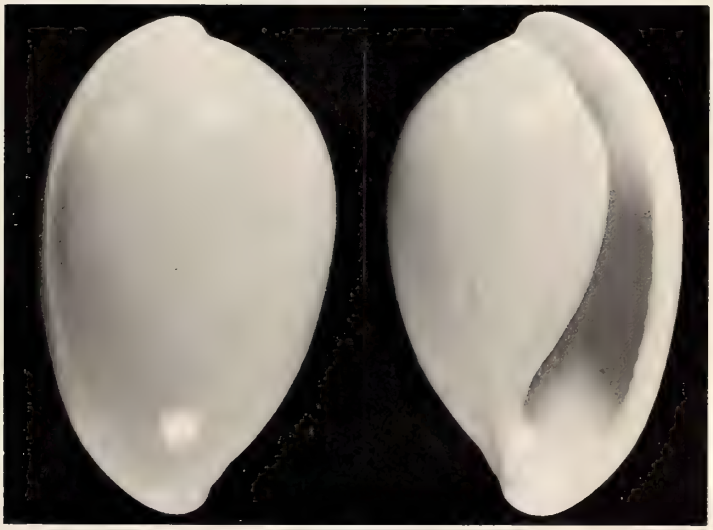

Figure *4*

Figure *5*

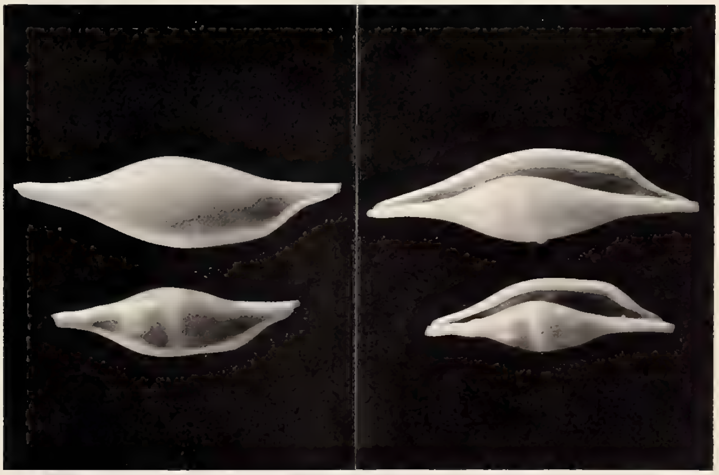

Figure *6*

lip stark white, with columella basic whitish-beige; terminal canals and tips darker orange-beige.

Measurements, holotype: L – 30.4; W – 11.0; H – 9.1 mm. (largest shell).

Measurements, paratype: L – 22.1; W – 8.1; H – 6.3 mm. (smallest shell).

Type Locality: Off Kaohsiung, SE Taiwan, East China Sea (22°44′ N; 120°21′ E). Trawled from 80 meters, 1971.

Distribution: Known only from type locality.

Holotype: Los Angeles County Museum of Natural History, California; No. LACM 1556. Paratypes: Cate (C 4029, 5 specimens; C 4046, 1 specimen).

Discussion: This new species probably most closely resembles *Phenacovolva (Turbovula) kashiwajimensis* Cate & Azuma, 1973, but differs from that species by its generally larger, more angularly inflated shell form and more reflected terminals; by its lack of transverse, incised dorsal striation; by its more discernible, flattened fossular area, with the unusual aspect of basic shell color being visible through thinned fossular nacre; by its more arched, bow-like, outer lip, and by its significant constant, different shell color, which seems characteristic of this species. The species is named for Ruth Greenberg, Malibu, California, who first sent the shells to the author for study.

Prionovolva ***nivea*** Cate, spec. nov.

(Hypotype: Figure *4*)
(Holotype: Cate, 1973: fig. 15b)

Description, holotype: Shell of medium size, oblong-ovate, thin, translucent, roundly inflated; dorsum smooth, glossy; terminals short, barely projecting; base roundly ovate, smooth, glossy, narrowing as a constricted ridge to the front; aperture broad, curving, enlarging toward the front; columella smooth, barely flattened, deepening as a fossula abapically due to presence of front base ridge; at rear a long, low, arching funiculum has two weak knobs; outer lip curving, narrow, edged, though thickened and shouldered above; lip teeth weak, somewhat indistinct, especially so adapically, crossing width of lip-edge at both terminals; shell color pure white over all.

Measurements, holotype: L – 16.7; W – 10.3; H – 7.0 mm. (ANSP No. 39423).

Measurements, hypotype: L – 13.6; W – 8.1; H – 6.6 mm. (C 3977).

Type Locality: New Caledonia (21°30′ S; 165°30′ E).

Distribution: New Caledonia to Japan [Off Hinomesaki, Kii, Japan; in 55 meters, (C 3977); leg. Shingo Habu, January, 1972.].

Holotype: Academy of Natural Sciences, Philadelphia: No. 39423.

Hypotype: Cate coll., C 3977.

Discussion: This new species may be compared with *Prionovolva pudica pudica* (A. Adams, 1854). In Cate, 1973 (p. 11; plt. fig. 15-b), specific recognition of this new species was avoided, being referred to as a possible variant of the Adams species. However, another almost identical specimen has been fished from deep water off the Kii peninsula, Japan, which makes possible reevaluation of the variant. *Prionovolva* ***nivea*** Cate, spec. nov., differs significantly from *P. pudica pudica,* having a more thinly formed shell; shell colorless, stark white over all, lacking the characteristic spot of pinkish-orange color always found at the base of each terminal beak (at the edge of the adjoining marginal callus) in *P. pudica pudica;* it also lacks the dorsal striation and transverse angular ridges; the rich rosy-pink color of *P. pudica pudica* is noticeably missing as well. The new name is derived from the Latin, *niveus,* meaning white as snow.

Delonovolva ***dolabra*** Cate, spec. nov.

(Figure *5*)

Description, holotype: Shell small, sub-translucent, thin, very narrowly ovate, truncate in front, pointed adapically; dorsum broadest sub-centrally, shiny, rather coarsely transversely incisedly striate over all; adapical terminal narrowly pointed, with exit of apertural canal on the right and outward, upward spiralling of funicular process extension to the dorsum forming a greatly distorted beak; base ovate, thinly nacred with striation visible beneath, narrowing constrictedly to the front; columella narrow, concave, and with the aid of a longitudinal adaxial carinal ridge deepening to a fossula abapically; aperture curving slightly, very narrow centrally, broadening openly to the front and back; outer lip broad, crudely dentate, slanting downward and inward, with larger teeth posteriorly; smaller, narrower, longer teeth anteriorly, protruding beyond periphery of outer lip edge; color somewhat glassy dorsally, with pale beige-white over most of the rest of shell, both terminals being darker beige-orange.

Measurements, holotype: L – 9.0; W – 3.0; H – 2.5 mm.

Type Locality: Off Hinomesaki, Kii, Japan (34°00′ N;

134°48′E), in 52 meters of water. Leg. Shingo Habu, March 1971.

Type: Los Angeles County Museum of Natural History: LACM No. 1557.

Discussion: This new species may be compared with *Delonovola serrula* Cate, 1973. Both species seem to have certain morphological aspects in common, yet they appear to be different enough to be separated specifically. *Delonovolva* ***dolabra*** is larger, with narrower and more elongate shell form; the adapical terminal process is not elevated nor reflected; the dentition on the outer lip is weaker, less developed; the shape of the funiculum and its arrangement is different; and this new species has color at the terminal tips and in the terminal canals. The name of this new species is derived from the Latin word for pickaxe, as these shells rather resemble the head of a miner's ax.

ADDENDA

It seems pertinent at this time to mention two rather important discoveries relating to the Ovulidae: until just recently the ovulid species *Phenacovolva (Calcarovula) piragua* (Dall, 1889) was known from only a single specimen. It can now be reported that two more live-taken specimens have been found (as reported by Kirk Anders, Fort Lauderdale, Florida), dredged from 72 m off Egmont Key [SW of Tampa, Florida] 27°31′N; 84°13′W); it seems two separate collections were made, one by William Lyons, the other by Douglas Wolf; (cf. Cate, 1973: fig. 241).

Phenacovolva (Turbovula) dancei Cate, 1973 (figure 6 herein: small shell, Bataan, Philippines; larger shell, off Taiwan), heretofore had been thought to have a rather limited living range confined to the northern Indian Ocean. It has recently been discovered in the waters off Kaohsiung, Taiwan, East China Sea (dredged from 80 meters of water). It is noteworthy to mention that shells from Taiwan seem to be much larger in dimension (L – 17 to 42; W – 6 to 12; H – 4 to 9 mm), and seem to display a change in color. The Indian Ocean and Philippine shells are roughly of the same size (L–17 to 21; W–5 to 6; H–4 to 6 mm). In the Taiwan habitat the shells of *P. dancei* seem to be much more abundant, and they grow to a far greater size. The shells are more thinly formed, almost translucent; their color varies from the normal mauve to a very light beige, although retaining the broad, transverse central band of off-white. The terminal tips are the usual orange, and the outer lip margin is white.

ACKNOWLEDGMENTS

I wish to express my appreciation to Joan Howland of Mackay, Queensland for specimens and other pertinent data; to Ruth Greenberg, Malibu, California, for specimens kindly donated; to Jean Cate for suggestions and photographs connected with this work; and to Bert Draper, Los Angeles, for certain other of the photographs herein.

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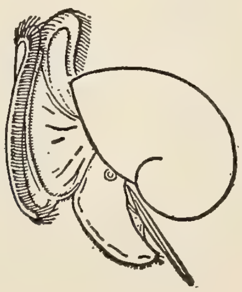

The Introduced Semelid Bivalve *Theora (Endopleura) lubrica* in Bays of Southern California

BY

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(2 Text figures)

DURING A SURVEY of the subtidal soft bottoms of the Lower Newport Bay, California, three Ekman-Birge Grab samples were collected on 14 July 1971 from a depth of 4 m in the Main Channel area adjacent to the Balboa Peninsula (Figure 1). The samples contained a total of 363 specimens of an unusual species of bivalve that could not be identified at the time. The three samples were subsequently combined and set aside for future reference. During June 1973 I sent several specimens to Dr. Eugene Coan for identification. He determined that the species was *Theora* (*Endopleura*) *lubrica* (Gould, 1861) and informed me that this represented the second record of the species on the Pacific Coast of the United States. It was first collected from Sunset Bay, California (Figure 1) during a benthic survey by the California Department of Fish and Game (HARDY, 1970). This record was cited by COAN (1973: 325) in a review of the Northwest American Semelidae. HARDY (1970: 22) considered that the introduction of *T. lubrica* to Sunset Bay probably occurred by U. S. Navy ships which frequent Anaheim Bay (Figure 1). The species has been previously reported (Habe and Ito, 1965) from Indonesia, Thailand, China, the Philippines and Japan (including Kiushu, Shikoku, Honshu, southwestern Hokkaido) in mud bottoms of the inner portions of bays.

On 6 July 1973 I resampled the area in the Main Channel of Lower Newport Bay. Thirteen samples were collected from the soft bottom, which could be described as a mixed substrate, having coarse silts (0.06 to 0.03 mm) as the predominant size fraction. Only three specimens of *Theora lubrica* were collected (each from a separate sample), indicating a mean density of 6.1 individuals per m^2. In a benthic survey of the Balboa Channel (Figure 1) by Marine Biological Consultants (1972a), *T. lubrica* (referred to as "?*Siliqua* sp. A") was collected at 3 of 6 stations. The mean density of 9.3 individuals per m^2 for the Balboa Channel area during September 1972 is comparable with the mean density of 6.1 specimens per m^2 for the Main Channel in July 1973 (Table 1).

Additional records for *Theora lubrica* (Table 1) were obtained by Marine Biological Consultants (1972b, 1973) from Sunset Bay (Huntington Harbour) and the Los Angeles Harbor (Figure 1). The low mean density value of 4.0 individuals per m^2 for *T. lubrica* (referred to as "*Siliqua* sp.") from Sunset Bay during August 1972 suggests a decrease in the population since the survey by HARDY (1970) in 1968–1969. High numbers of *T. lubrica* (referred to as "?Tellinidae B, unident.") were recorded from Slip 5 in the East Basin Channel of Los Angeles Harbor. One would expect that the species is established in other parts of Los Angeles Harbor, and possibly in Long Beach Harbor and Alamitos Bay. The present records for *T. lubrica* summarized in Table 1 suggest that the species is established at low population densities in at least 3 bays in Southern California. The very high mean density of 1,384 individuals per m^2 for the Main Channel of Lower Newport Bay in July 1971 could represent a period of time during which an unusually successful repopulation of the area had occurred.

The following description of *Theora lubrica* is provided to aid in species identification. The majority of specimens examined from Newport Bay, Sunset Bay and Los Angeles Harbor ranged from about 6 to 10 mm in length. The largest specimen measured 12.8 mm and was collected from Los Angeles Harbor. Externally, the valves are smooth and shiny with fine concentric ribbing, and the periostracum is not evident. The valves gape slightly at the anterior and posterior ends. An internal rib, extending from a point just anterior of the beaks toward the antero-ventral margin, is normally evident externally through the thin, translucent valves. The most prominent internal features of the valves (Figure 2) include the ribs directed antero-ventrally in each valve, a small and bulbous resilium and the bifid cardinal tooth in the left valve.

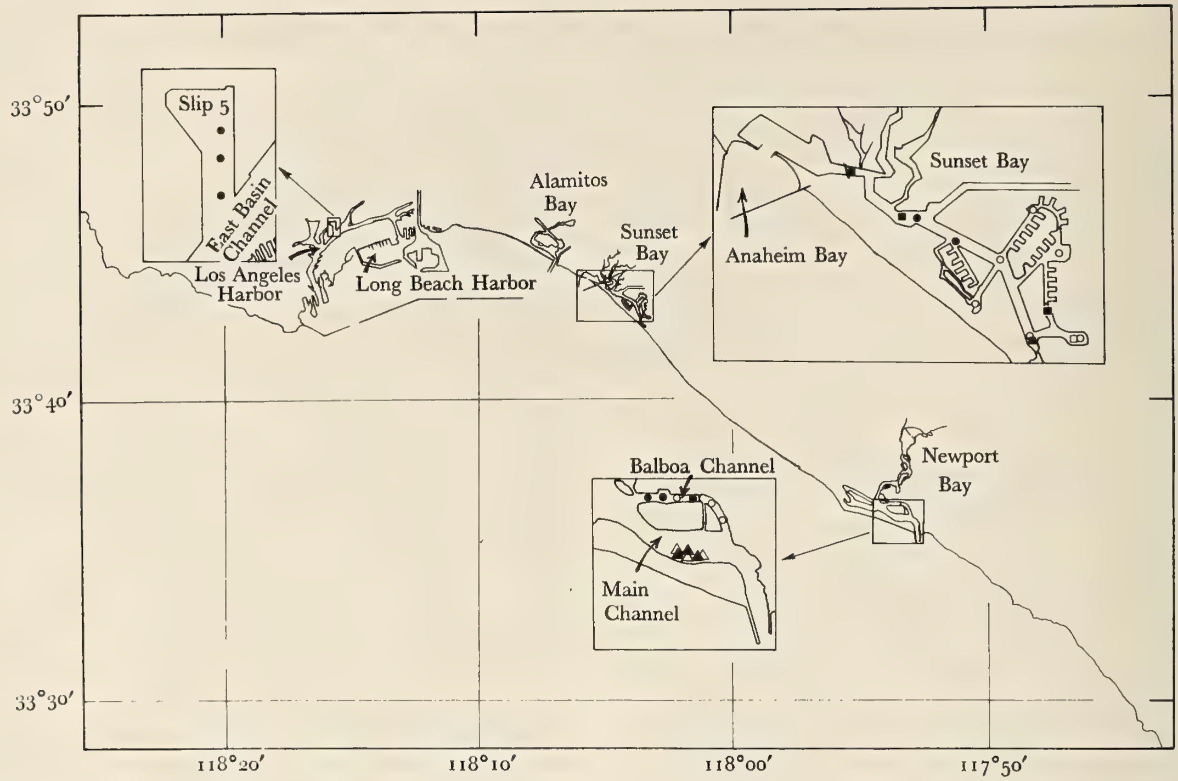

Figure 1

Station locations for benthic studies in Los Angeles Harbor, Sunset Bay, and Lower Newport Bay. Stations occupied by Marine Biological Consultants in Los Angeles Harbor, Sunset Bay, and Balboa Channel of Lower Newport Bay are indicated by circles. Station locations in Sunset Bay for the Fish and Game study (HARDY, 1970) are indicated by squares. Stations occupied by Seapy in Main Channel, Lower Newport Bay are indicated by triangles. Solid symbols represent stations at which *Theora lubrica* was collected, while open symbols represent negative stations.

Specimens of *Theora lubrica* from the July 1971 collection have been sent to the California Academy of Sciences, Stanford University and the Los Angeles County Museum of Natural History. A set of specimens has been deposited in the Museum of Systematic Biology, University of California, Irvine.

ACKNOWLEDGMENTS

Appreciation is expressed to Mr. Ronald Rathburn for collection of the grab samples from Lower Newport Bay during July 1971; to Dr. Eugene Coan for reviewing the manuscript and providing preliminary sketches of the interior of the valves; to Mrs. Margaret Mooney for translation of the section of Habe and Ito (1965) concerned with *Theora lubrica;* and to Marine Biological Consultants, Costa Mesa, California, for their assistance and the loan of specimens.

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Table 1

Records of *Theora lubrica* from Southern California Waters

Location	Sampling Date	Sampling Device	Area of Sample (m^2)	Number Samples	Number Specimens	Range in No. Specimens per Sample	Mean No. Specimens per m^2	1 S. E.	Source of Data
Los Angeles Harbor East Basin Channel Slip 5	August 1973	Shipek Grab	0.042	9	39	0 - 7	105.7	±17.7	Marine Biological Consultants (1973)
Sunset Bay	October 1968 January 1969	Orange Peel Grab	0.051	10	6	0 - 4	11.8	± 7.8	Hardy (1970)
Sunset Bay	August 1972	Shipek Grab	0.042	24	4	0 - 2	4.0	± 2.7	Marine Biological Consultants (1972b)
Lower Newport Bay Main Channel	July 1971	Ekman-Birge Grab	0.038	3	363	-	1 384.2	-	Seapy (herein)
Lower Newport Bay Main Channel	July 1973	Ekman-Birge Grab	0.038	13	3	0 - 1	6.1	± 3.2	Seapy (herein)
Lower Newport Bay Balboa Channel	September 1972	Shipek Grab	0.042	18	7	0 - 3	9.3	± 4.4	Marine Biological Consultants (1972a)

Hardy, Robert A.
1970. The marine environment of Upper Newport and Sunset Bays, Orange County, California. Resources Agency Calif. Dept. Fish & Game, MRR ref. no. 70-10; 84 pp. (August 1970)

Marine Biological Consultants
1972a. Biological survey of Balboa Channel, Newport Harbor, California. Unpubl. Reprt. 44 pp.; 1 text fig.; 4 tables; 3 appendices (7 September 1972)
1972b. Baseline study of Huntington Harbor. Unpubl. Reprt., 73 pp.; 3 text figs.; 9 tables; 5 appendices (23 October 1972)
1973. Survey of the biota in Slip 5, Los Angeles Harbor. Unpubl. Reprt., 19 pp.; 2 text figs.; 4 tables; 1 appendix (23 August 1973)

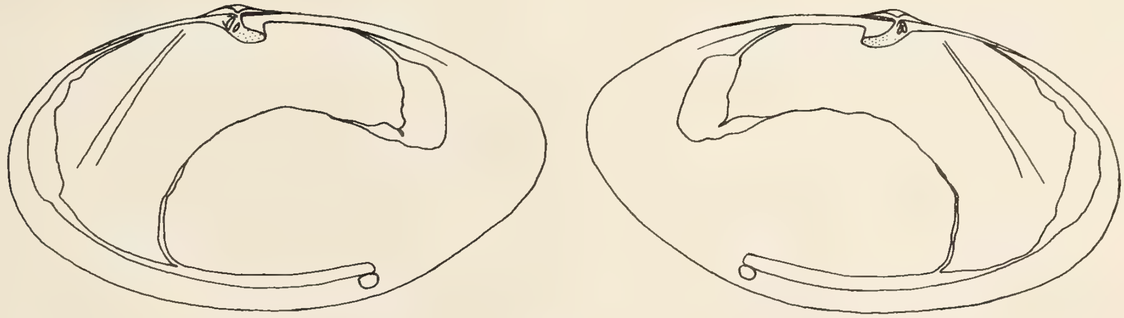

Figure 2

Internal view of the valves of *Theora lubrica*; 10.8mm

Vertical Intertidal Distribution of *Mytilus edulis*

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(3 Text figures)

INTRODUCTION

Factors controlling the distribution of the mussel *Mytilus edulis* Linnaeus, 1758 in the intertidal zone appear to be divisible into: 1) intra- and interspecific space and site competition; 2) fluctuations in physical environmental factors; and 3) predation by mobile predators. The study reviews previous ecological studies on *M. edulis*, reports new data from experiments on interspecific competition between *M. edulis* and the acorn barnacle *Balanus glandula* Darwin, 1854 and summarizes the ecological stresses on *M. edulis* for different parts of its vertical intertidal distribution. In examining interspecific competition for space between *M. edulis* and a coexisting species we chose a clearly delimited example where the ecological niche contains two dominant species. The middle part of the intertidal zone along the more protected part of the northern Pacific coast of North America includes two filter feeders, *M. edulis* and *B. glandula*, which occur in great abundance in overlapping zones in the middle and higher parts of the intertidal zone. Their ecological and geographical distributions raise questions as to whether they are competing with each other for space and, if so, the nature of the mechanism which allows them to coexist. We present data on one aspect of competition: survivorship in established populations where the two species coexist. We did not examine questions of interspecific competition of larval settlement.

Mytilus edulis has a worldwide distribution in the temperate regions and, like other mussels, is a filter feeder that spends its adult life attached by a threadlike byssus to crevasses or irregularities on hard substrates either in or slightly below the intertidal zone. In California spat commonly colonize suitable habitats as high as 0.6 m below high water (Harger, 1967). Larval settling of *M. edulis* is well documented by Engle & Loosanoff (1944), Graham & Gay (1945), Chipperfield (1953) and Seed (1969a); the latter reported the onset of spawning when water temperatures rise from 9.5°C to 12.5°C.

Information is sparse on the distribution of *Mytilus edulis* as affected by either competition or predation. Landenberger (1967) found that predation by starfish determined the lower limits of mussels on pier pilings, and Landenberger (*op. cit.*), Feder (1955, 1959), and Mauzey *et al.* (1968) established that, although *Pisaster ochraceus* (Brandt, 1835) will eat a wide variety of animals, it has a clear preference for *M. edulis*. Intraspecific competition for space in *M. edulis* spat settling on dense adult beds was determined by Seed (1969b) but he made no mention of interspecific competition. The competitive relationships between *M. edulis* and *M. californianus* Conrad, 1837 in areas of ecological overlap between the quieter, muddier waters of bays and estuaries and the more exposed waters of the coast were discussed by Harger (1967, 1968, 1970a, 1970b, 1972a, 1972b) and Harger & Landenberger (1971). The two species adapt to the two extremes of wave energy and turbidity; *M. edulis* has a thinner shell, weaker byssal threads, and more readily crawls away from confining pressures of closely packed individuals, reflecting the adaptations of the quieter water species.

Near Point Atkinson, British Columbia, Canada, *Mytilus edulis* is found on much of the rock surface generally below, but overlapping, the lower part of the distribution of *Balanus glandula*. Large *M. edulis* (about 2.0 to 4.5 cm)

occur only low in the intertidal zone and are not common. Small *M. edulis* (less than 1 cm) extend up to a height of 0.9 m above mean tide level. Specimens of *M. edulis* are mostly in a single layer, except in well protected concavities in the rock surface where they may form clumps. At high densities individuals are oriented with their umbones directed toward the rock surface and the posterior margin of the shell directed outwards. At lower densities the ventral margin is parallel with the rock surface.

Balanus glandula occurs in the upper part of the intertidal zone from Baja California, Mexico, to the Aleutian Islands (Barnes & Barnes, 1956). On the San Juan Islands, Washington, *B. glandula* settle principally from late May through August (Connell, 1970). Although settling occurs throughout the entire intertidal zone, Connell (*op. cit.*) found that predators, mainly species of *Thais*, eliminate all *B. glandula* from the lower part of the intertidal zone. At Ladysmith, British Columbia, and at La Jolla, California, growth of *B. glandula* takes place mainly during the spring and summer months with little or no growth in winter (Barnes & Barnes, *op. cit.*).

Near Point Atkinson *Balanus glandula* is found above as well as within most of the range of *Mytilus edulis*. Hummocking of *B. glandula* occurs but most individuals retain their patelliform shape. Population densities of both *B. glandula* and *M. edulis* are not uniform but often exceed 32 individuals per 7.5 cm².

METHODS AND RESULTS

The study was conducted on an area of protected shore, approximately one-third of a mile west of Point Atkinson, B.C., Canada, on the north side of Burrard Inlet, from July to December, 1970. This site permitted use of tide data published for Point Atkinson by the Canadian Hydrographic Service (1970). Human tampering was eliminated by using beach adjacent to private property. The cliffs and large rocks at this location are exposed to moderate wave action which increases considerably during winter storms. During these storms, numerous large floating logs were observed to present an additional hazard to the survival of mussels and barnacles in the intertidal zone.

At Point Atkinson the annual seawater temperatures range from approximately 6.3°C to 20.2°C, reaching spawning levels of 11 to 12.5°C about the beginning of May, and salinities range from 20.3‰ to 29.4‰. These ranges span the extremes of mean monthly temperatures and salinities recorded during 1966 at Entrance Island, Departure Bay and East Point, the three locations closest to the study area for which these data are available (Canadian Oceanographic Data Center, 1968). Point Atkinson has a mixed, mainly diurnal tide, a mean tidal range of 3.1 m and a mean water level of 3.0 m above Canadian tidal datum.

COMPETITION EXPERIMENTS

Competition between *Mytilus edulis* and *Balanus glandula*.

Five intertidal areas (Table 1) near Point Atkinson were selected for competition experiments with *Balanus glandula* and *Mytilus edulis*. Each area had 4 sites (2 caged sites and 2 uncaged sites) and each site was approximately 768 cm.² Test sites were selected at several heights above mean tide level (MTL). In Table 1, original counts of *M. edulis* and *B. glandula* are given in columns 3 and 4. Treatment is summarized in column 5. In some sites all *B. glandula* were removed and in some of these a few *M. edulis* were destroyed accidentally. Those *M. edulis* unavoidably removed with the barnacles while setting up the experiments are recorded in the treatment column but are not included in the calculations of mussels lost. Selected sites were covered by plastic cages. Data in columns 6–13 are counts made in mid-September, October, November and December, 1970. The cage over site 1c was lost in a storm on November 20, 1970. *M. edulis* on sites 4a and 5b and both *M. edulis* and *B. glandula* on site 5a were destroyed by floating logs during storms. *Mytilus edulis* in the uncaged sites 1d, 2c and 3d were eaten by sea stars. Columns 14–17 show the fraction and percentage of *M. edulis* lost from caged and uncaged sites from high, middle and low intertidal positions. Cages consisted of flexible plastic bowls (30 cm in diameter and 7.5 cm in height) with 800 1 cm holes per bowl. About 49% of the cage surface was covered and excluded *Pisaster ochraceus* without apparently greatly altering wave action or wave circulation. Cages were attached with stainless steel sheet metal screws through the lip of the bowl into plastic screw anchors which had been cemented into holes star-drilled into the rock.

Effects of intraspecific competition were minimized by choosing sites on which *Mytilus edulis* was in a single layer rather than in clumps. Specimens of *Balanus glandula* were removed with a probe and a scalpel from one of the two caged sites and one of the two uncaged sites of each area, care being taken not to disturb adjacent mussels. Records were kept of mussels unavoidly removed because they were attached to barnacles. Sites were rinsed thoroughly with seawater to wash away remaining pieces of *B. glandula* and thereby reduce the attraction of predators.

Initially a sixth area was also chosen for study, 0.6 m below mean tide level. However, all the mussels and barnacles on uncaged sites at this location were eaten by sea

stars three days after the experiments had begun, and within the same time both caged sites were covered with the green alga, *Ulva,* which restricted free water circulation. Reluctantly, this area was abandoned. Other algae growing in the intertidal zone (*Fucus, Porphyra* and *Enteromorpha*) did not interfere with the experiments.

The proximity of the areas and particularly the sites within each area minimized variation of physical factors. Control sites in each area were checked to determine the effect of the cages as well as the effect of removing *Balanus glandula.* Monthly counts, taken at approximately the same time each month, were made on both uncaged and caged sites (the latter by removing the cage). The count noted the position of individual mussels and barnacles on acetate sheets attached to a wooden frame. Different colored ink distinguished the position of barnacles and mussels.

Results for competition experiments (Table 1) give the original count, the treatment, and the monthly counts of *Mytilus edulis* and *Balanus gladula* and summarize the data of the fraction of *M. edulis* lost at the high, middle and low experimental areas. Because the cage on site 1c was destroyed by logs in a storm on November 20, 1970, the November data for this site were used in the calculation for Table 1. Data for uncaged sites with *B. glandula* removed and *B. glandula* not removed were not considered separately because a large proportion of the uncaged sites were totally denuded of both species by either sea star predation or log damage. The total numbers of *M. edulis* lost from caged and uncaged sites are recorded to separate predation and damage due to physical factors from direct species competition.

Differences in the proportions of *Mytilus edulis* lost from caged and uncaged sites from high, middle and low

Table 1

Results of experiments testing interspecific competition between *Mytilus edulis* and *Balanus glandula*

Asterisks (*) indicate sites used in calculations

Height above M.T.L. (m)	Site	Original Count August		Treatment	
		Mytilus edulis	*Balanus glandula*		
0.75	1b	2471	773		
	1d	586	342	*Balanus glandula* removed	
	1c	788	97		caged
	1a	1476	584	*B. glandula* + 13 *Mytilus edulis* removed	caged
	4d	747	385		
	4a	509	309	*Balanus glandula* removed	
	4b	447	274		caged
	4c	588	194	*Balanus glandula* removed	caged
0.35	3d	709	84		
	3a	793	446	*B. glandula* + 31 *M. edulis* removed	
	3c	637	248		caged
	3b	1247	753	*Balanus glandula* removed	caged
	5a	826	463		
	5b	652	363	*B. glandula* + 76 *M. edulis* removed	
	5d	851	740		caged
	5c	898	468	*Balanus glandula* removed	caged
0.03	2b	1071	419		
	2c	778	499	*B. glandula* + 24 *M. edulis* removed	
	2d	595	654		caged
	2a	662	437	*B. glandula* + 32 *M. edulis* removed	caged

experimental areas, were analysed statistically, using a nonparametric Z test. This method tests the significance of the difference between two proportions and returns a Z score, which measures the likelihood that the difference has occurred by chance (BRUNING & KINTZ, 1968). Using a one-tailed test, results from the caged and uncaged sites at the three separate heights are different, *i.e.* a larger proportion of *M. edulis* are lost from uncaged sites (level of significance $\propto = .001$).

The same statistical procedure, applied to the difference between caged sites where *Balanus glandula* had been removed and caged sites where *B. glandula* had not been removed, showed that a greater proportion of *Mytilus edulis* was lost where *B. glandula* was not removed than where *B. glandula* had been removed ($\propto = .001$). The proportion of *M. edulis* lost from caged sites decreased with decreasing intertidal height ($\propto = .01$).

Comparison of data (Table 1) for caged sites where *Balanus glandula* were removed and caged sites where *B. glandula* were not removed suggests that interspecific competition between *B. glandula* and *Mytilus edulis* is a factor in the distribution of mussels, particularly at high intertidal levels. The proportion of *M. edulis* lost from high, middle and low sites where they were growing in close association with *B. glandula* was greater than for similar sites where *B. glandula* had been removed ($\propto = .001$). In interspecific competition between *Chthamalus stellatus* (Poli, 1791) and *Balanus balanoides* (Linnaeus, 1758), *B. balanoides* smothered, undercut or crushed *C. stellatus* and the greatest mortality occurred during the season of most rapid growth of *B. balanoides* (CONNELL, 1961). Our data show the greatest loss of *M. edulis* occurred in November and December, a season of slow growth for both *B. glandula* (BARNES & BARNES, 1956) and *M. edulis* (SEED,

Table 1 [continued]

Results of experiments testing interspecific competition between *Mytilus edulis* and *Balanus glandula*

September		October		November		December		Fraction of *Mytilus edulis* lost			
Mytilus edulis	*Balanus glandula*	*Mytilus edulis*	*Balanus glandula*	*Mytilus edulis*	*Balanus glandula*	*Mytilus edulis*	*Balanus glandula*	uncaged	caged	caged *B. glandula* & *M. edulis*	caged *B. glandula* removed
2458	773	2443	773	2440	773	2031	768	*			
342	–	340	–	0	–	0	–				
781	97	768	97	641	87	0	0	999	* 231	* 213	18
1463	–	1462	–	1460	–	1455	–	3727	* 3286	1235	* 2051
739	385	731	385	39	351	37	346	* 27%	7%	17%	1%
509	–	107	–	63	–	60	–	*			
445	274	438	274	427	261	381	258		*	*	
588	–	585	–	585	–	578	–		*		*
704	84	700	84	27	52	19	48	*			
761	–	759	–	759	–	748	–	*			
611	248	606	248	585	234	542	230		*	*	
1245	–	1245	–	1243	–	1236	–	704	* 156	212	* 20
823	463	818	463	71	30	0	0	1471	3633	1488	2145
575	–	573	–	573	–	0	–	48%	4%	14%	1%
838	740	831	740	819	726	734	721		*	*	
898	–	898	–	897	–	889	–		*		*
1064	419	1064	419	1043	416	787	409	* 285	67	54	13
754	–	753	–	0	–	0	–	1071	1225	654	630
582	654	588	654	574	639	541	637		*	*	
628	–	628	–	628	–	617	–	27%	5%	* 8%	* 2%

1969b). Mortality of *M. edulis* apparently was not the result of crushing, smothering or undercutting by *B. glandula* during periods of rapid growth.

Observations from July to December, 1970, on other *Mytilus edulis* and *Balanus glandula* growing in close association below the mean tide level suggest that there the effects of interspecific competition may be reversed. In contrast to the single layered distribution of *M. edulis* and *B. glandula* that commonly occurs above the mean tide level, an outer layer of *M. edulis* may cover a mixed layer of *M. edulis* and *B. glandula.* Because a stronger pull is required to remove mussels from low in the intertidal zone (Glaus, 1968), those individual *M. edulis* that crawl out may be able to come together to form a layer with highly intertwined byssal threads, making this outer layer more stable. In this situation, *M. edulis* would have an advantage in competition for food and *B. glandula* may be smothered.

Intraspecific Competition

Intraspecific competition for space is an important factor in the distribution of *Mytilus edulis* in the lower part of its intertidal zonal occurrence (Seed, 1969b). However, the sites selected for this study were at or above mean tide level where *M. edulis* formed only a single layer on the rock surface. The small number of mussels lost from cage sites where *Balanus glandula* had been removed (Table 1) suggests that intraspecific competition was not significant at these sites.

OTHER EXPERIMENTS

Connell (1961) suggested that the upper limit of most intertidal organisms is determined by physical factors. Two transplant experiments with *Mytilus edulis,* designed to test this hypothesis, were started on July 2, 1970, and the survivors were counted at the end of the experiment on December 30, 1970.

One hundred *Mytilus edulis* taken from throughout the intertidal range were gently pulled from rock surfaces on the beach near Point Atkinson and placed on a flat, horizontal rock surface 1.2 m above the mean tide level, 0.3 m above the highest naturally occurring level of *M. edulis* and covered with a cage. Another hundred specimens from immediately west of Kitsalano Beach on the south side of False Creek, were placed adjacent to those from Point Atkinson. Individuals that did not attach within three days were removed from the transplant cages. During these three days 78 out of one hundred transplanted specimens from Point Atkinson attached and 72 out of one hundred specimens from Kitsalano attached. Seventy-six, or 97.4% of the mussels from Point Atkinson, and 71, or 98.6% of those from Kitsalano were living at the end of the experimental period. These high survival rates of caged *M. edulis* transplanted 0.3 m above the species' highest natural occurrence indicate that the upper limit may not be determined entirely by duration of submergence (and the availability of food) or by certain other physical-chemical factors normally considered responsible for determining the upper limit. Apparently larval stages of *M. edulis* are unable to colonize these higher levels although transplanted adult specimens have no major difficulty surviving there. The cages used in the experiments may have created some shading and thereby influenced dessication rates; however, it is not apparent that they had any great effect.

Data from our competition experiments suggest that most *Mytilus edulis* are dislodged and removed by strong physical wave action associated with storms. Harger (1968) has shown that in clumps of mixed mussel species *M. edulis* exhibits a "crawling out" behavior which results in their becoming arranged on the outside of the clump and, thereby, enjoying an initial competitive advantage over *M. californianus.* Because this characteristic behavioral trait of *M. edulis* is exhibited when objects press against it, population densities, as high as those occurring at Point Atkinson, probably caused *M. edulis* to "crawl out" during the season of most rapid growth. Once on the outside of the clumps and away from the rock surface, individual *M. edulis* would be more vulnerable to the forces of wave action (Jones & Demetropoulos, 1968). In addition, individual mussels are less firmly attached than mussels growing together on the rock surface where byssal threads of several mussels become interwoven. Data presented in Table 1 suggest that normal wave intensity during the growing season was not sufficient to remove *M. edulis* that "crawled out" but that storms in November and December were sufficiently intense to remove large numbers of *M. edulis* that had been competing with *Balanus glandula* (sites where *B. glandula* had not been removed). Glaus (1968) reported an increase in the average pull required to remove specimens of *M. edulis* from rock surfaces at successively lower levels in the intertidal zone. This may be the reason why a smaller proportion of *M. edulis* were lost from the lower caged sites where *B. glandula* had not been removed (Table 1).

Observations indicate that large numbers of *Mytilus edulis* below the mean tide level are eaten by sea stars and the lower limit of *M. edulis* is probably determined by predation. *Pisaster ochraceus* was particularly abundant but its distribution was extremely variable. The gregarious

nature and mobility of this sea star introduced so many variables that tidal and seasonal data on its predatory behavior and relative effects on *M. edulis* populations were not analyzable. The density of *P. ochraceus* varied greatly but reached as high as 70 individuals per m².

Connell (1970) showed the lower limit of *Balanus glandula* on San Juan Island, Washington, was between higher low water and lower low water and was determined by several species of the predaceous whelk *Thais*. *Thais* drills a small, readily identifiable hole through the shell of *Mytilus edulis* (Seed, 1969b). One hundred empty shells collected low in the intertidal zone at Point Atkinson lack these holes and indicate *Thais* predation is not a factor in the present experiments. All the experimental sites at Point Atkinson are at or above mean tide level and well above the lower limit of both *B. glandula* and *M. edulis*. This suggests, as noted by Connell (1970), an insufficient time between tidal changes for *Thais* to move that far up in the intertidal zone, find and feed on either species.

AGE AND GROWTH DATA

Size and age composition of experimental *Mytilus edulis* populations were estimated from one hundred specimens from each of three areas. These specimens were measured and the number of conspicuously visible growth lines recorded (Figures 1–3). Specimens from Area A were living 0.60 to 0.75 m above mean tide level and specimens from area B were living 0.15 m below mean tide level. Specimens from area C were empty, intact hinged shells collected from piles that accumulated beneath nearly vertical surfaces on which *Pisaster ochraceus* was an abundant predator. Growth rate studies by Harger (1972b) for populations of *M. edulis* on Ellwood Pier, Santa Barbara, California, suggest that shell lengths of about 5 cm are reached in one year, 6 to 7 cm in two years, 7 to 8 cm in three years and 9 to 10 cm in seven years. Actual growth rates of *M. edulis* in the Point Atkinson area have not been determined. *Mytilus edulis* grows more rapidly in lower positions in its intertidal zonal distribution and in subtidal situations than in the higher part of its distribution (Couthard, 1929; Harger, 1967; and Edwards, Meaney & Davies, 1969). Slower growth rates are apparently related to more exposure and variation in available food supply and temperature fluctuations. The development of growth lines in *M. edulis* is at present incompletely understood. Harger (1967) considered growth inhibiting factors such as exposure to wave shock and pressure of competition in mussel clumps were positively corre-

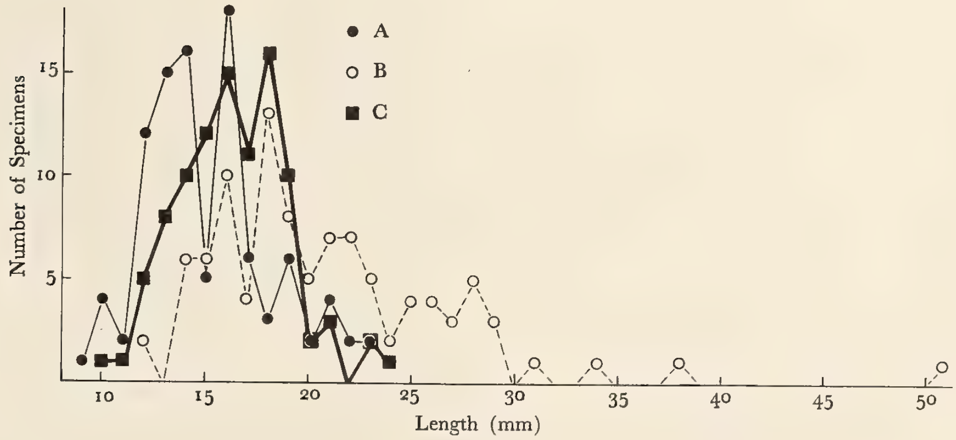

Figure 1

Size distribution of specimens of *Mytilus edulis* from three intertidal levels, Point Atkinson, British Columbia. A, 0.60 to 0.75 m above mean tide level; B, 0.0 to 0.15 m below mean tide level; C, empty shells beneath bank of *Mytilus edulis* on which *Pisaster ochraceus* were actively feeding

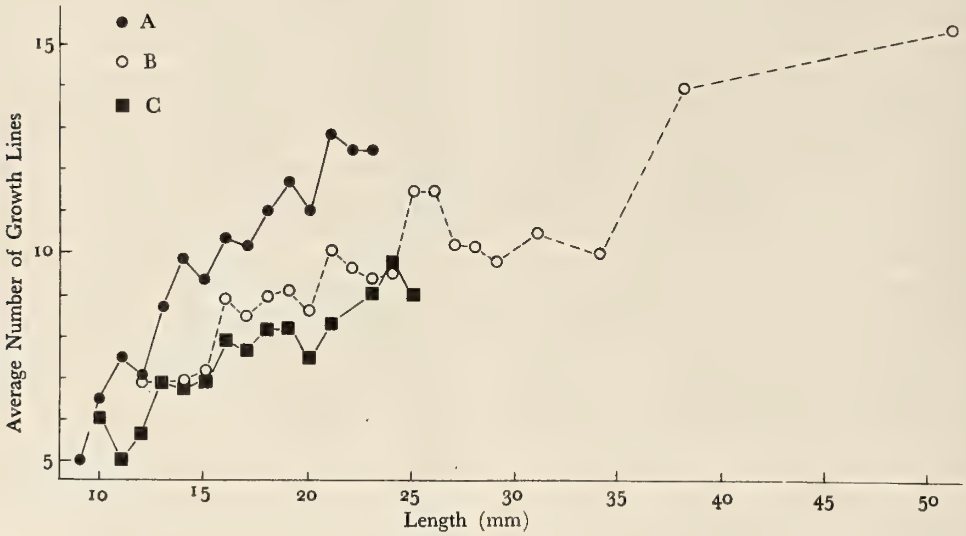

Figure 2

Average number of growth lines on *Mytilus edulis* from three intertidal levels, Point Atkinson, British Columbia. See Figure 1 for positions of A, B, and C

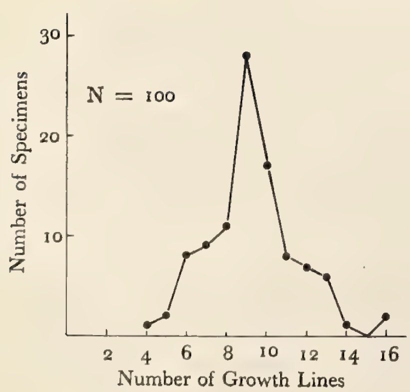

Figure 3

Size distribution of 100 specimens of *Mytilus edulis* (sample C in Figures 1 and 2) from piles of empty shells beneath a bank on which *Pisaster ochraceus* were actively feeding, Point Atkinson, British Columbia

lated with numbers of growth lines. SEED (1968) concluded that growth lines could represent annual increments depending on the seasonal conditions.

Although data collected from the three samples of *Mytilus edulis* at Point Atkinson (Figures 1–3) are not extensive, they are consistent with the findings of previous studies. Comparison of length and number of growth lines between the three measured samples (Figures 1–3) show intertidally higher *M. edulis* are smaller and have more growth lines at the same length than those growing lower in intertidal areas, suggesting growth is conditioned by Harger's short term environmental factors.

SUMMARY

The vertical intertidal distribution of *Mytilus edulis* is apparently controlled by a number of ecological interactions. The upper limit, about 0.6 m below mean high tide, seems to be related to survival of settling spat because transplanted adults are able to survive 0.3 m above their normal natural occurrence. Above mean tide level, com-

petition experiments suggest active competition for space between *M. edulis* and *Balanus glandula* which results in some of the *M. edulis* crawling out during the late summer growing season and the subsequent plucking of these individuals by wave action during autumn and early winter storms.

Below the mean tide level, *Mytilus edulis* grows more rapidly, commonly forms dense mats two layers thick which smother *Balanus glandula* and develops more wave resistant intertwined byssal threads. The lower limit of *M. edulis* is determined by the increasing stress of predation by sea stars, particularly *Pisaster ochraceus,* and, at other localities, species of the whelk *Thais.* Although *M. edulis* is occasionally reported from subtidal positions, such populations are not common because of the preference of *P. ochraceus* for *M. edulis.* The duration of intertidal exposure seems the critical factor in this predation.

In addition to the number of *Mytilus edulis* lost through interspecific competition with *Balanus glandula* and predation by *Pisaster ochraceus,* large numbers of both *M. edulis* and *B. glandula* are destroyed by logs that were observed to wash against the shore during the winter storms. Harger (1967, 1972b) suggested *M. edulis* and *M. californianus* coexisted in mussel clumps because of the complexity and unpredictability of environmental stresses, particularly winter storms. Hutchinson (1957) stated the competitive exclusion principle is unlikely to apply where there is clearing of sites by high death rates or with the formation of transient sites by random small catastrophes in the biotope. At Point Atkinson loss of large numbers of *M. edulis* by interspecific competition with *B. glandula* and predation by *P. ochraceus,* combined with removal of large numbers of both *M. edulis* and *B. glandula* from the intertidal rock surface by the destructive force of floating logs, appears to provide adequate sites each year for the settling of both *B. glandula* and *M. edulis,* thereby allowing the coexistence of these species in the intertidal zone.

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A Method for Estimating Live Weight and Body Length from the Shell of *Aplysia willcoxi* Heilprin, 1886

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(2 Text figures)

Obtaining reliable size measurements of mollusks which possess only thin, internal shells has often posed problems due to the extreme contractility of the animals. The problems are compounded when one tries to compare data from living and dead specimens. In my studies of the sea hare *Aplysia willcoxi* Heilprin, 1886, at Cedar Key, Florida, I found that references to the size of the animals rarely describe the position of the animals when measured (Andrews, 1971; Eales, 1960; Gray, 1940; Gunter & Hall, 1963 and 1965; Hackney, 1944; Heilprin, 1886; Moore, 1961; Zinn, 1950). Only one report includes data on shell lengths (Zinn, *op. cit.*). No references were found to the weights of the sea hares.

I attempted to find a consistent relationship between live weight, body length, and shell length of freshly caught sea hares. This relationship would enable me to obtain a good estimate of live weight and body length from the shells of dead specimens.

Seventy-five sea hares were weighed and measured within two hours of capture. Each sea hare was blotted on paper towels and weighed to the nearest 0.1 g on a triple beam balance. To obtain a standard measurement of body length, each sea hare was placed in a large enamel pan filled with seawater. The animal was then prodded into swimming. In this position the animal was extended and measurements to the nearest centimeter were made when viewing the sea hare from directly above. The body length was taken as the distance from the tip of the oral tentacles to the tip of the tail.

From 13 of these animals the shells were extracted and the lengths were measured to the nearest millimeter. This was done while the shells were still wet since the lightly calcified shells tend to shrink upon drying.

Figure 1 plots the Log. body weight against Log. body length. The least squares regression line fits the equation

$$\text{Log. body length} = 0.36 \text{ Log. weight} + 0.4414.$$

($L = 2.76\ W^{0.36}$; correlation coefficient, r, = 0.95; standard error of the slope = 0.01; N = 75).

Figure 2 is a plot of the Log. body weight against Log. shell length. The data fit the regression equation (N = 13; r = 0.98; standard error = 0.01; $SL = -1.08\ W^{0.27}$)

$$\text{Log. shell length} = 0.27 \text{ Log. body weight} - 0.0349.$$

By using a Student's t test, both slopes were found to be significantly different from 0 ($p<0.01$ and $p<0.001$, respectively).

By using these two graphs, it is possible to estimate the live weight and body length from the shell of a dead *Aplysia willcoxi*, provided that the shell has not been allowed to dry out. Since the shells of *Aplysia* do not appear to undergo any significant shrinkage or distortion in formalin or 70% alcohol, these relationships should also be useful in working with museum specimens. Similar allometric equations probably exist for other members of the genus *Aplysia* and should be useful to students of the group.

Despite the author's efforts to standardize the animals' position when the body lengths were measured, it is still this parameter which is the most difficult to measure ac-

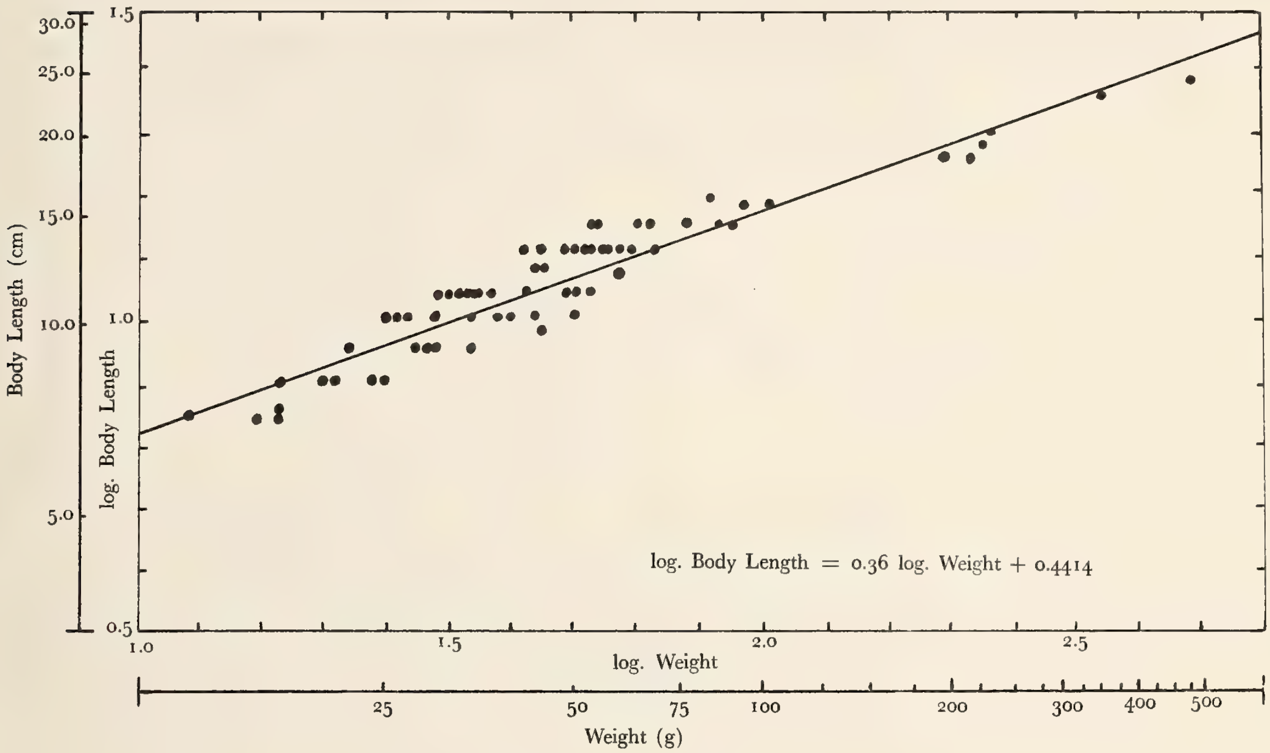

Figure 1

Log. body length plotted against Log. live weight

curately. In the normal range of positions that a sea hare may adopt there is an estimated maximum change of ⅓ of the total body length. Although it is difficult to measure a moving animal, it is my belief that greater accuracy is gained by having each animal in the same position. However, weight and shell length are probably the best indicators of the size of *Aplysia*.

Zinn (1950) has noted that the *Aplysia willcoxi* from Rhode Island waters appear to be larger than those reported from further south. The shells measured by Zinn ranged from 5.8 cm to 9.4 cm. The largest sea hare recorded in the present study was 550.1 g and had a shell length of 5.3 cm. It would be interesting to see if data from New England specimens of *A. willcoxi* would fall on the allometric curves.

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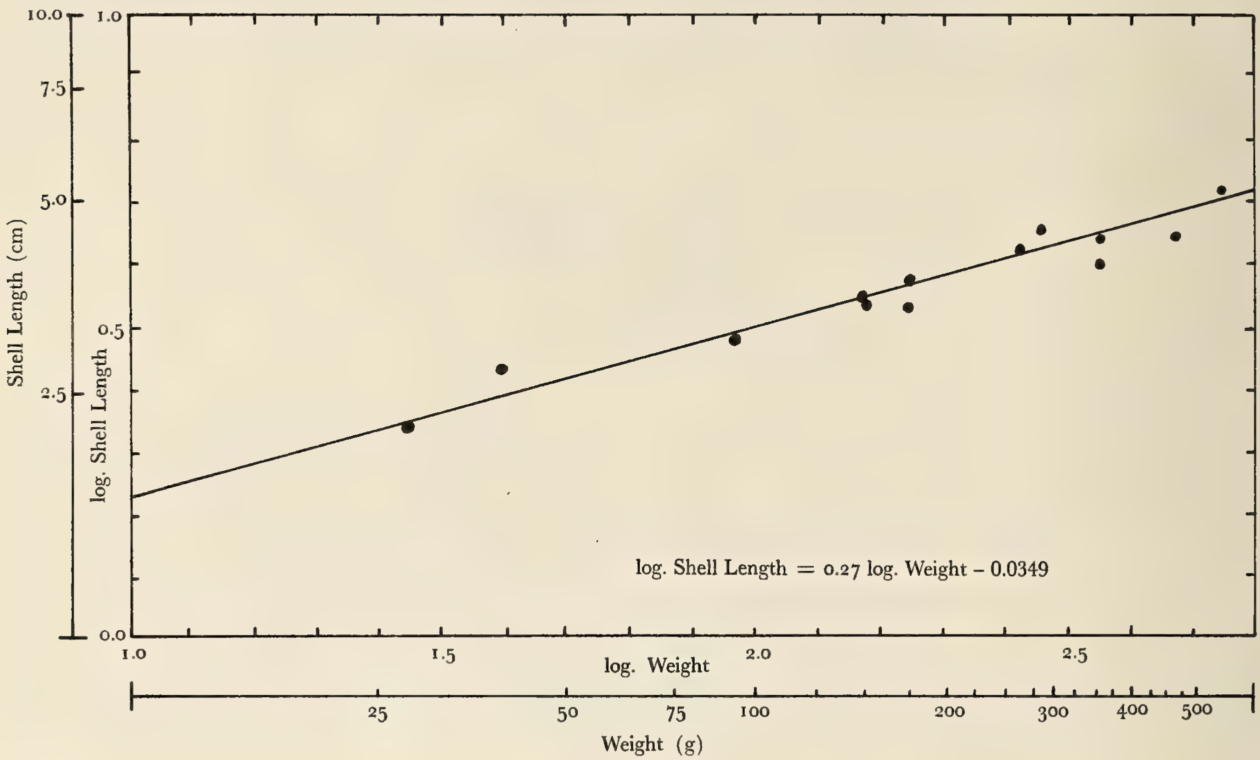

Figure 2

Log. shell length plotted against Log. body weight

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Spawning, Development and Growth in the Pulmonate Limpets *Siphonaria pectinata* Linnaeus, 1758 and *Siphonaria alternata* Say, 1822

BY

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(3 Text figures)

INTRODUCTION

Two species of the pulmonate limpet *Siphonaria* occur in South Florida; *S. pectinata* (Linnaeus, 1758) is common on the east coast as far south as Key Largo and *S. alternata* (Say, 1822) is the common species from Key Largo southward in the Keys. In some areas, with rocky intertidal substrate, *Siphonaria* is the dominant gastropod (over 1800 per m² at one site on Key Largo). Because *Siphonaria* feeds by rasping microalgae from the substrate it is influential in the erosion of beach rock (Craig *et al.*, 1969) and prevents the establishment of sessile plants and animals on the shore (Bastida *et al.*, 1971).

Voss (1959) reported observations on several aspects of the biology of *Siphonaria pectinata* including: feeding habitat, spawning, larval development (with descriptions of the egg, veliger and juvenile stages), environmental and geographical variation, geographical distribution and growth. The effects of *S. pectinata* on beach rock were reported by Craig *et al.* (1969).

In this paper the reproductive, developmental and growth patterns of *Siphonaria pectinata* and *S. alternata* are compared and the relationships between the two species are discussed.

MATERIALS AND METHODS

Spawning activity was observed in the field for a period of one year by removing and counting new egg masses on sections of beach rock 1.0 m² in area. Egg counts for *Siphonaria pectinata* were made twice weekly on a limestone rock at Bear Cut near the School of Marine and Atmospheric Science of the University of Miami. For *S. alternata* egg counts were made at irregular time intervals on the intertidal rocky platform near Tavernier, Florida (25°02′ N; 80°30′ W). Both sections were centered at the midtide level.

Each month a group of 30 adult limpets of each species was brought into the laboratory and maintained in jars of 900 ml capacity (10 limpets per jar) to note any egg laying. Gonad smears were made each month from another group of 20 limpets of each species. Regular observations were also made on the egg laying activities of laboratory-reared populations of *Siphonaria*.

Growth studies were initiated in two ways. Egg masses of *Siphonaria alternata* were collected from laboratory-reared limpets. Within 72 hours after hatching juveniles were removed from the containers and transferred to rocks from which all macroinvertebrates and macroalgae had been removed. The rocks were then placed in a 120 cm × 120 cm × 30 cm tidal box which emptied and filled automatically to simulate a tidal cycle. A cycle of 12 hours of light and 12 hours of darkness was maintained.

Because the development of *Siphonaria pectinata* involves a prolonged planktonic phase, and settlement of the larvae could not be achieved in the laboratory, it was necessary to strip sections of seawall of all macroinvertebrates and macroalgae and then recover juvenile limpets from the wall within one day after settling. This method provided the youngest limpets possible, but their exact age was not known. The juvenile limpets were transferred to rocks which were placed in the tidal box.

RESULTS

Reproduction

The spawning patterns for *Siphonaria pectinata* and *S. alternata* from September 1971 to August 1972 are shown in Figure 1. *S. pectinata* spawned from mid-September until the first week in May with peak egg laying occurring in December and January. Fluctuations in the number of eggs deposited were roughly related to the tidal cycle with the highest deposition occurring during spring tides (Figure 1). *S. pectinata* reared in the lab spawned during the same months as those in the field.

The spawning record for *Siphonaria alternata* is not as complete as the record for *S. pectinata* because of the greater elapsed time between egg counts for the former species (Figure 1). However, egg masses from *S. alternata* were found in the field in every month of the year with the highest counts being made in February and March. Fluctuations in egg mass counts for *S. alternata* were considerably greater than for *S. pectinata.* No clear correlation between egg laying periodicity in *S. alternata* and the tidal cycle could be determined because of an inadequate number of counts. In the laboratory oviposition by *S. alternata* also occurred throughout the year and no correlation between egg laying rhythms and the lunar cycle was observed.

Dissections of the reproductive systems and gonadal smears of *Siphonaria pectinata* made during December showed that: a well defined gonad (with some spermato-

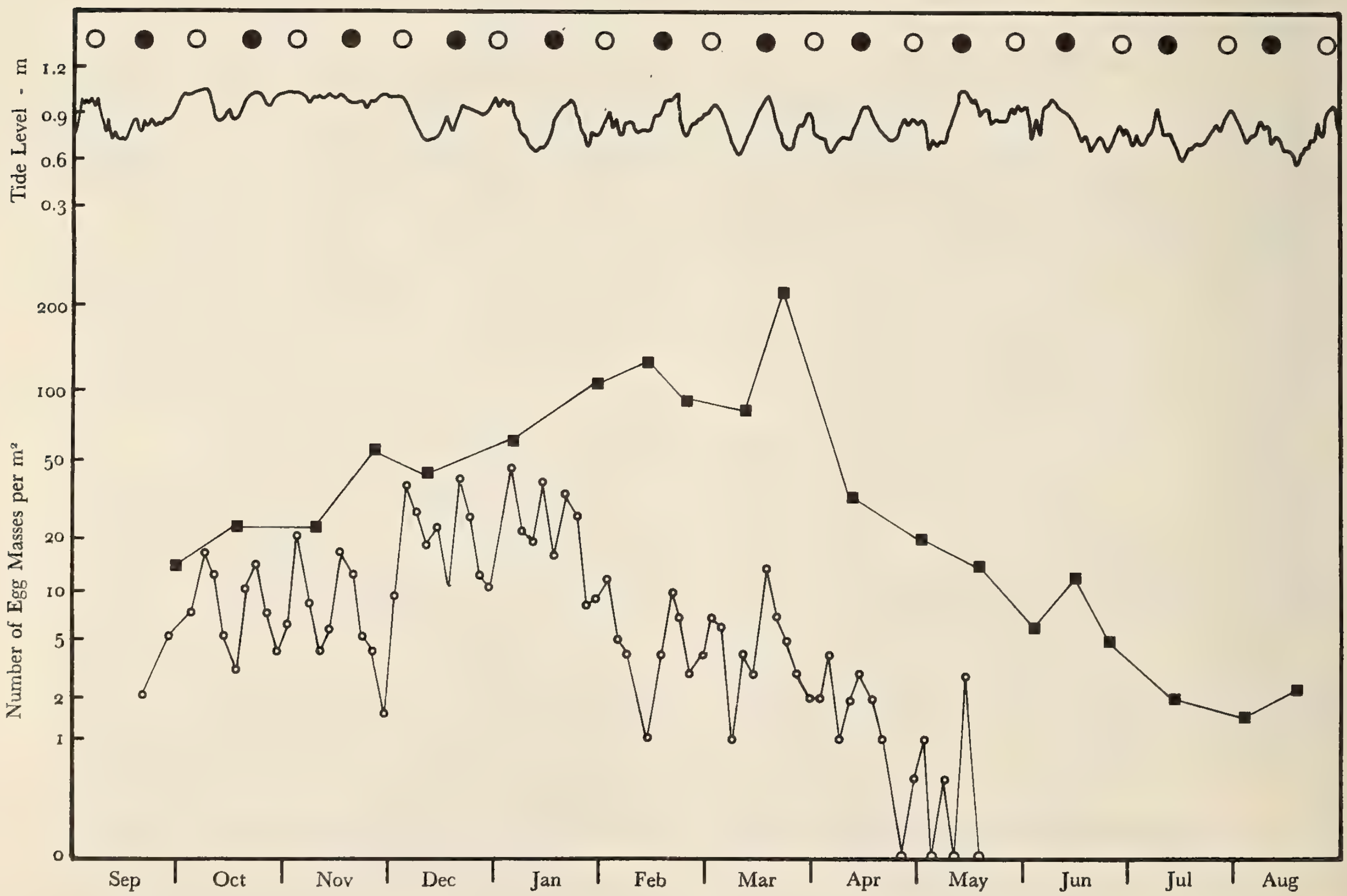

Figure 1

Semi-log plot of the number of egg masses of *Siphonaria pectinata* (○) and *Siphonaria alternata* (■) deposited per m² of intertidal rock from September 1971 to August 1972. Upper curve shows tidal level in meters above mean low water.

zoa) was present in individuals with a mean length of 5.5 mm (approximately 110 days after settling), the first eggs appeared at about 7.0 mm (approximately 140 days after settling), egg laying began at about 9.0 mm (approximately 170 days after settling), and limpets over 20 mm long are essentially females with a few spermatozoa present in the ovotestis. All of the mature limpets had large numbers of developing eggs present in the gonad during periods of high egg laying activity. During the months when egg laying was suspended the ovotestis was reduced to about one-third its active size and relatively few spermatozoa were the only gametes present.

In *Siphonaria alternata* a well defined gonad was present when the mean length of the shell was about 4.5 mm (approximately 120 days old), the first ova appeared at about 5.5 mm (approximately 145 days old), and egg laying began about 7.0 mm (approximately 200 days old). The numbers of developing eggs in the ovotestis of mature *S. alternata* of similar size were variable throughout the year.

Development

Table 1 shows the comparative numbers and sizes of the offspring of *Siphonaria pectinata* and *S. alternata*. The egg masses of *S. pectinata* are generally longer than those of *S. alternata* and contain approximately 5 times as many eggs per unit length. Both the egg (mean diameter 0.15 mm) and veliger (mean length 0.28 mm) of *S. alternata* are larger than the corresponding stages of *S. pectinata* (0.10 and 0.15 mm). The egg incubation periods of the two species are similar (approximately 17 days for *S. pectinata* and 15 days for *S. alternata* at a mean temperature of 23.1° C), but the durations of the pelagic periods are quite different (Table 1). *Siphonaria pectinata* has a planktotrophic veliger which swims continuously and lives for about 11 days without feeding. (Attempts to induce settlement of the larvae of this species in the laboratory were unsuccessful when they were fed on *Chlorella* and offered a substrate occupied by limpets of the same species.) The veliger of *S. alternata* is a feeble, intermittent swimmer which will generally settle on the surface of a glass container and loses its velum within three days after hatching when reared in filtered seawater.

Growth

Figure 2 shows the growth curve of laboratory-reared *Siphonaria pectinata*. At the time of settling the mean length of the limpets was 0.3 mm, and they grew at a rate of approximately 1.5 mm per month until they were about 8.7 mm long (165 days after settling). From 8.7 to approximately 10 mm length (205 days after settling) the rate was about 1.0 mm per month and limpets over 10 mm long increased in length at the rate of about 0.6 mm per month.

The growth curve for laboratory-reared *Siphonaria alternata* is shown in Figure 3. At the time of settling the mean length of the limpets was 0.28 mm. For the next 107 days (to mean length 4.5 mm), they grew at approximately 1.2 mm per month. The growth rate declined to approximately 1.0 mm per month for the next two months (to

Table 1

Comparison of: size of developmental stages, number of eggs per mm egg mass, incubation period and longevity of veligers of *Siphonaria pectinata* and *Siphonaria alternata*

	Siphonaria pectinata	*Siphonaria alternata*
Size of egg mass		
Length	8 - 40 mm (mean 20 mm)	7 - 19 mm (mean 12 mm)
Width	2.0 mm	2.0 mm
Height	2.0 mm	2.0 mm
Number of eggs per mm mass (mean)	210	40
Egg diameter (mean)	0.10 mm	0.15 mm
Veliger size (mean)	0.15 mm	0.28 mm
Duration of incubation period (mean)	17 days	15 days
Duration of pelagic period (mean)	11 days [1]	3 days

[1] could not be induced to settle in the laboratory

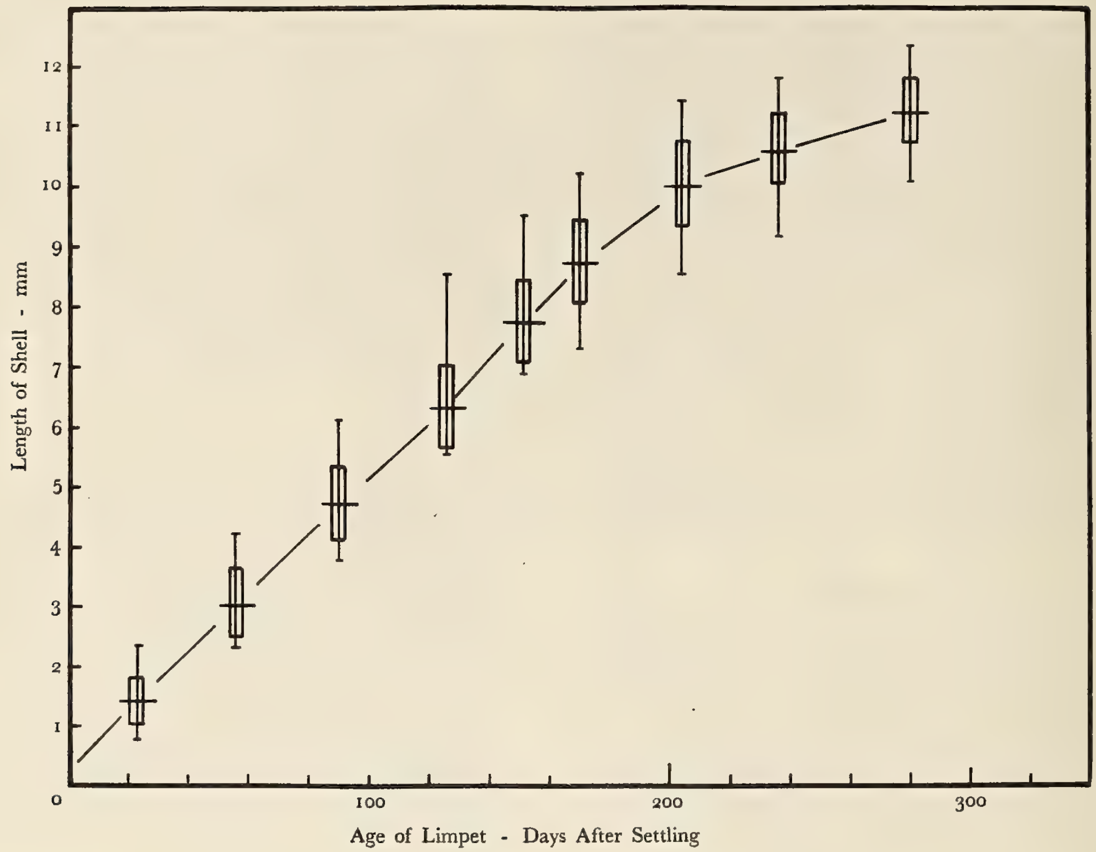

Figure 2

Absolute growth rate of laboratory reared *Siphonaria pectinata* after larval settling. Vertical lines represent range, horizontal lines the means, and vertical bars the standard deviations of the shell lengths of 50 individuals at each time interval.

mean length 7.0 mm). Limpets over 7.0 mm long (approximately 200 days old) grew at the rate of about 0.6 mm per month.

Both species of *Siphonaria* underwent a decline in growth rate during the period between the time the first eggs appeared in gonadal smears and the time the first eggs were deposited, *i. e.*, 7.0 to 9.0 mm in *S. pectinata* and 5.5 to 7.0 mm in *S. alternata*.

DISCUSSION

Voss (1959) reported that *Siphonaria pectinata* spawned only from December through March when the surface water temperatures in South Florida were at the low range for the year (21° to 23.3° C), and she suggested that the southern distribution limit for the species is affected by whether the winter minimum is cool enough for spawning. My observations showed that *S. pectinata* spawned from late September, when the minimum temperature was 28.3° C, to early May, when the minimum temperature was 24.4° C. This suggests that *S. pectinata* spawns over a relatively wide temperature range and that its spawning, and probably also its southern distribution limit, may be controlled by factors other than, or in addition to, temperature.

Although spawning in *Siphonaria alternata* was concentrated in the winter months of January through March,

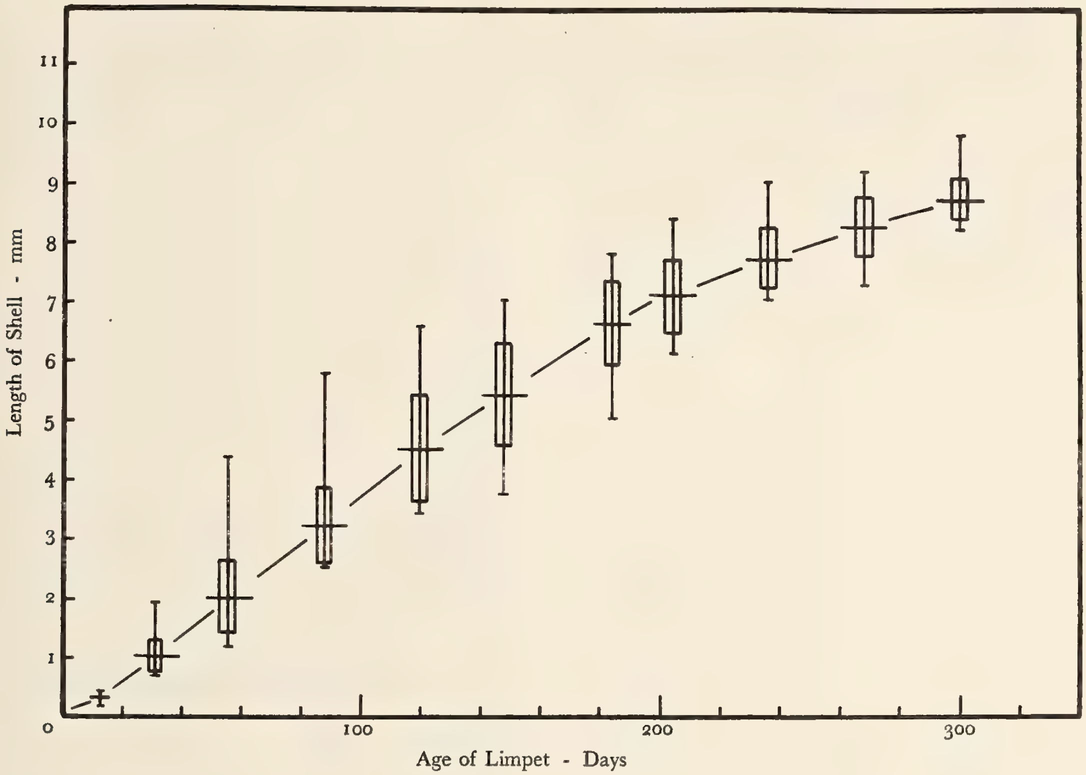

Figure 3

Absolute growth rate of laboratory reared *Siphonaria alternata.* Vertical lines represent range, horizontal lines the means, and vertical bars the standard deviations of 75 individuals at each age interval.

the population examined contained some reproductively active individuals during every month of the year. Year-around spawning may afford *S. alternata* a competitive advantage over *S. pectinata* where the geographical ranges of the two species coincide.

A comparison of the developmental patterns in the two species of *Siphonaria* shows that *S. pectinata* produces more numerous but smaller eggs and larvae than *S. alternata.* These interspecific differences are consistent with the observation that *S. pectinata* has a prolonged and *S. alternata* has an abbreviated planktonic phase, a correlation common among benthic marine invertebrates (Mileikovsky, 1971).

The differences in development may explain the distributional differences between the two species. *Siphonaria pectinata* is widely distributed in the warmer latitudes on both sides of the Atlantic (for a more detailed range description see Voss, 1959). Hubendick (1947) considered the spread of siphonarid larvae over great distances to be extremely improbable. However, Scheltema (1971) has calculated, from the known velocities of North and Tropical Atlantic surface currents, that a benthic gastropod with a planktonic phase of three months duration (or less if the larvae display delayed metamorphosis) could exhibit transoceanic dispersal. If the planktonic phase of *S. pectinata* is of sufficient duration its amphi-Atlantic distribution could be explained. More information on this portion of the life history of this species would be welcome.

Hubendick (1947) gives the range of *Siphonaria alternata* as East and South Florida, Bermuda, Cuba and Mexico. The localized distribution of this species is likely a consequence of its abbreviated veliger period.

From monthly size-frequency studies Voss (1959) reported the following growth rates for *Siphonaria pectinata* of different sizes: hatching to 6.0 mm long 2.0 to 2.5 mm per month, 6.0 mm long 1.2 mm per month, 11.0 mm long 0.6 mm per month and 14.0 mm long 0.4 mm per month. The lower early growth rate which I observed for *S. pectinata* (1.5 mm per month from settling to 8.7 mm long) probably resulted from the handling the limpets received when they were transferred from the seawall to the laboratory. Field and laboratory observations showed that *S. pectinata* grows more rapidly and achieves a larger maximum size (approximately 25 mm) than *S. alternata* (maximum size approximately 15 mm).

In the Florida Keys Stephenson & Stephenson (1950) reported finding *Siphonaria pectinata* as far south as Plantation Key and only *S. alternata* on the southern Keys, West Summerland and Key West. Both species were present only on the oceanic side. Voss (1959) found *S. alternata* as far north as Soldier Key in Biscayne Bay and reported that *S. pectinata* was the dominant species on Key Largo, "where specimens of *S. alternata* were found scattered among the more numerous *S. pectinata*." I have found a few large *S. pectinata* in populations as far south as Lower Matecumbe Key and *S. alternata* as far north as North Key Largo on both the oceanic and Florida Bay sides of the Keys. On North Key Largo the population is about 70% *S. alternata*.

Comparison of occurrence records shows that the two species of *Siphonaria* have undergone local changes in distribution and relative abundance in recent years. *Siphonaria alternata* has become more numerous in the northern Keys and has invaded Florida Bay. Both species are found in a similar vertical zone on the shore, *i. e.*, concentrated at the midtide level, and they are likely competing for space and food wherever they coexist. Owing to differences in larval development *S. alternata* may have a competitive advantage. As pointed out by Mileikovsky (1971), benthic species with prolonged pelagic larval periods are subject to large scale fluctuations in their adult populations due to such changing planktonic conditions as predation and food resources. It follows that *S. pectinata*, with its prolonged pelagic phase, would show greater instability in the age structure of its adult population as a result of these fluctuations, than would *S. alternata* with its abbreviated veliger period. In fact, at North Key Largo, where both species occur, only adult *S. pectinata* (over 13 mm long) were found but *S. alternata* of all ages were present. Mileikovsky (*op. cit.*) has concluded that one of the disadvantages for species with prolonged pelagic development is "reduction of the ability to withstand invasions of competitive species and to cope with higher levels of competition during periods of poor settlement." A further competitive advantage for *S. alternata* would seem to accrue from reproductive activity, of at least some members of its population, throughout the year.

Siphonaria alternata may be more adaptable to changing water conditions than *S. pectinata*, as suggested by the apparently recent spreading of the former species to the Florida Bay side of the Keys. *Siphonaria pectinata* has previously been recorded from the oceanic side only. Voss (1959) concluded that *Siphonaria* was unable to tolerate the changing conditions of temperature and salinity characteristic of the Bay. What role abiotic factors play in determining the local distributions of the two species is not clear.

Following future changes in the populations of *Siphonaria* in the upper Florida Keys should provide interesting information on the biological relationships between these two species.

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The Food and Feeding Habits of the Cuttlefish *Sepiella inermis* (Férussac & d'Orbigny)

BY

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INTRODUCTION

THE CEPHALOPODS have been known for their economic potential as food. They are also of immense biological interest, being highly evolved molluscs with a degree of learning ability comparable to that of some vertebrates. Most of the investigations made in this group were on the species *Sepia officinalis* (WELLS, 1962) and "only in less than half a dozen do we know anything about the general biology, physiology and reproduction" (ADAM & REES, 1966).

Practically no studies have been conducted on the cuttlefishes in waters around Singapore. The aim of the present investigation is to study the food and feeding habits of *Sepiella inermis* (Férussac & d'Orbigny), a species of cuttlefish found in local waters.

BIDDER (1966) stated that all known living cephalopods studied are active predators, swimming in pursuit of their prey. *Sepia officinalis* has been observed to feed on crabs, prawns, shrimps and fish by many workers (MESSENGER, 1968; WELLS, 1962, and WILSON, 1946). FÉRUSSAC & D'ORBIGNY (1848) also observed *Sepiola atlantica* feeding on small molluscs and fish, while *Idiosepius* sp. was seen feeding on gammarids (SASAKI, 1929). But no report has been made so far on *Sepiella inermis.*

MATERIALS AND METHODS

Sepiella inermis is identified by its ovate mantle with chromatophores concentrated in the mid-dorsal region; it can be distinguished from other cuttlefishes by the series of shiny white elliptical markings on the margin of the mantle at the base of the fins. These ellipses numbered from 7 to 9 pairs. Just anterior to the junctions where the fins meet posteriorly is a round brown spot marking the position of a gland which opens on to the ventral side via the glandular pore. The cuttlebone of this species lacks the rostrum which is present in other *Sepia* species (ADAM & REES, 1966).

Specimens were collected from a kelong, a fixed palisade trap, using light as a lure to attract fish, in the Straits of Johore, situated to the north of Singapore Island. *Sepiella inermis* were caught individually with a scoop net. Special care was taken not to injure the specimens which were required live for laboratory studies. Slight injury of the thin epithelium often resulted in a high mortality in the laboratory in less than 3 days. The animals were transported to the laboratory in polyethylene bags containing a few centimeters of seawater and an atmosphere of oxygen.

In the laboratory live animals were carefully kept in clean plastic tanks (35 cm $\times$ 18.3 cm $\times$ 21.5 cm) with a layer of about 4 cm of coral sand and 3 l of seawater. Rubber gloves were used when handling or transferring the animals. Temperature was kept at about 25 to 27° C. Continuous aeration of the water was essential because the oxygen consumption of the animals is high and the cephalopod respiratory mechanism is not adapted to cope with any downward fluctuation of oxygen, even of the most temporary nature (WELLS, 1962). Care was taken not to excite the animals whose sudden movements normally resulted in injury due to collision with the tank walls. Sudden flashes of light from lamps and movements of objects or people were kept at a minimum. To minimise the effects of these factors, the aquarium tanks were kept behind curtains and covers.

Animals for the study of stomach contents were preserved in 5 to 10% formalin immediately after capture.

Temporal variations in diet and feeding habits of adult and juvenile *Sepiella inermis* were evaluated by the monthly percentage occurrence of the types of food consumed as well as the monthly feeding intensities by examining the stomach contents of the specimens caught in the field. At the same time, experiments in the laboratory were designed to test the food selectivity of *S. inermis* with different types and sizes of prey and the results were compared with the field data.

Stomach Contents

For the study of stomach contents, specimens were caught at fortnightly intervals at the collection site. The mantle length, the distance between the tip of the mantle and the junction of the fins at the posterior end, and the mantle width at the broadest region of each specimen were measured. Each individual was considered as immature or juvenile when no sexual organs were detected. Mature specimens were identified from the sexual organs, such as testes and genital duct in the males and ovaries and nidamental bodies in the females.

A total of 71 stomachs were examined and the percentage number feeding was calculated for each month as a measure of monthly feeding intensity of the population from the formula

$$\frac{\text{number of stomachs with food}}{\text{total number of stomachs examined}} \times 100$$

The specimens examined were divided into 3 categories: juveniles, adult males, and adult females.

The degree of feeding for each individual was also noted and classified in the following manner:

E – 'empty' – when the stomach was empty

S – 'slight' – when the stomach was not distended and there was little food

M – 'medium' – when the stomach was slightly distended with food

H – 'heavy' – when the stomach was fully distended with food and usually occupied $\frac{1}{3}$ of the mantle cavity

and the proportions of stomachs for each degree of feeding were also calculated for each month.

The percentage monthly occurrence of each food type consumed by the animal was calculated by

$$\frac{\text{number of stomachs with food type}}{\text{total number of stomachs examined}} \times 100$$

The percentage monthly occurrence of the food item was determined for 2 size categories of *Sepiella inermis*: those smaller than 25 mm (immature) and those larger than 25 mm (mature) in mantle length. The 25 mm length coincided with the length of the smallest mature specimen examined.

Laboratory Experiments

In the laboratory 2 experiments were carried out: one to determine the selectivity of *Sepiella inermis* towards prey types and the other to determine the selectivity towards the prey size.

Animals used were acclimated for a period of at least 3 days. They were then starved before the start of each experiment. This was to minimize the differences in the degree of hunger. Each experimental animal was kept in a separate tank so that no complications, such as interference from or social facilitation between predators was present (Holling, 1966).

To determine food preference, prey types offered to the predator were fish (*Poecilia reticulata*), prawns (*Acetes* sp.) and crabs (*Dotilla* sp.). These prey animals corresponded quite closely to the type and size of prey consumed by *Sepiella inermis* in the natural environment. At the start of the experiment, 10 of each prey type were offered simultaneously to the predator. After half an hour, the remainder of each type of prey left uneaten was noted. Two sizes of cuttlefish and 2 individuals of each size class were studied. The sizes within each prey type offered were kept as constant as possible:

Poecilia reticulata – 20 mm standard length
Acetes sp. – 3 to 5 mm carapace length
Dotilla sp. – 20 mm carapace width

In the experiment designed to study the effect of prey size on food preference, only *Poecilia reticulata* were offered because it was the only prey type that was readily eaten by all sizes of cuttlefish. The 2 sizes of *Poecilia reticulata* offered were 10 mm and 30 mm standard length, Two sizes of predators, 20 mm and 40 mm mantle length, were studied. On the first day of the experiment, a mixed offer consisting of 5 10 mm and 5 30 mm *P. reticulata* was presented. Two days later, a pure offer consisting of 10 10 mm fish was made and subsequently, after another 2 days a pure offer of 10 30 mm prey animals was made. At the end of half an hour after each offering, the remaining number of prey animals of each size group was noted. The intervals of 2 days between each 2 feedings were made to insure that all the predators were properly starved. Three replicates were conducted for each size group of predators.

RESULTS

Predatory Behaviour

The capture of fish by *Sepiella inermis* is similar to that described for the capture of prawns by *Sepia officinalis* (Messenger, 1968). The whole predatory behaviour is composed of 3 main phases: attention, positioning, and seizure.

When the prey (*Poecilia reticulata*) was offered, the eyes of *Sepiella inermis,* which normally rested half-buried

in the sandbed, were seen to focus on the prey and follow its movements for a few seconds. Then the cuttlefish elevated itself slowly out of the sandbed and swam towards the prey. At the same time, during this "attention" phase, a general darkening of the body was observed.

The cuttlefish approached the prey slowly and positioned itself at a distance about its own body length away from the prey. In a few individuals this positioning was followed by the raising of its first and second pair of arms. It is suggested that this behaviour, which was also observed by MESSENGER (1968) in other species, probably serves to distract the prey. However, in the majority of *Sepiella inermis*, this raising of arms was not observed. Whenever the prey moved, the cuttlefish followed, thus always positioning itself in line with the prey.

In some individuals the prey was seized soon after positioning while in others the predator remained stationary in midwater for some time before attacking. In healthy cuttlefish during the seizure phase the tentacles were projected at the prey with great precision. However, the tentacles were not so effectively employed to capture the prey by cuttlefish which had been kept in aquaria for more than 4 weeks. These cuttlefishes appeared to have lost their ability to project their tentacles with accuracy. The projected tentacles did not seem to extend to their fullest and often fell short of the prey. These cuttlefishes often capture their prey with their arms instead. This change in behaviour was often observed in cuttlefish a few days prior to their death. This symptom may be indicative of an unhealthy cuttlefish.

When crabs (*Dotilla* sp.) were offered, the attention and the positioning phases were similar to those described for the capture of fish, except that a longer time was spent hovering above the crab. The crab was seized either with the tentacles or with the arms. BOYCOTT (1958) and WILSON (1946) reported that attacks on crabs were made from the posterior end of the crab, probably to avoid the pincers. However, observations of *Sepiella inermis* confirmed MESSENGER's (1968) report that head-on attacks were also made. The direction of attack was probably determined by the size of the prey's pincers and the state of hunger of the predator.

MESSENGER (1968) noted that *Sepia* discards the antennae and rostrum of prawns and the carapace, chelae, and walking legs of crabs. However, in starved *Sepiella inermis* all parts of the crab and fish were consumed, while individuals which had already consumed a few prey specimens often discarded fish heads.

MESSENGER (1968) suggested that prey animals were probably killed by cephalotoxins injected into them by the predator. However, *Poecilia reticulata* removed from *Sepiella inermis* after the first bite were found to survive up to 15 minutes, which is longer than that recorded for prawns seized by *Sepia* sp. (MESSENGER, *op. cit.*). It would appear that the cephalotoxin of *Sepiella inermis* was either absent or not as potent as that found in other species of cuttlefish.

Food Preference and Feeding Intensity

Generally the monthly percentage number feeding in the juvenile, adult male and adult female *Sepiella inermis* was high throughout the period of this study (Table 1) indicating that feeding was continuous and probably non-seasonal. The females showed the highest percentage number feeding, with the lowest percentage number shown by the juveniles. This low percentage feeding index of the juvenile could probably be due to the inavailability of suitable prey animals of the right size.

The juveniles fed moderately in the months of April and July, and heavily in May and June as shown by the monthly feeding intensity (Table 2). About 50% of the mature males generally showed heavy feeding in all the months except in April. The mature females generally

Table 1

Percentage Feeding in Juvenile, Adult Male and Adult Female *Sepiella inermis*

Month	Juveniles		Adult Males		Adult Females	
	% feeding	No. exam.	% feeding	No. exam.	% feeding	No. exam.
April	100	2	100	4	100	2
May	50	2	100	17	78.5	8
June	50	4	50	2	100	2
July	100	2	89	9	100	2
August	–	–	75	8	100	4

showed moderate feeding, with some feeding heavily in August. Apparently, the males are much more voracious feeders than the females and the juveniles.

The monthly percentage occurrence of food items in the stomachs examined (Table 3) clearly indicates a preference for prawns (*Acetes* sp.) by the smaller *Sepiella inermis* throughout the months of this study. Both fish (mainly *Stolephorus* sp.) and prawns (mainly *Acetes* sp.) were consumed by the larger cuttlefish. Both food items fluctuated slightly in their monthly occurrence in the diet of the predator. Crabs were found in the stomachs only in May. The crabs eaten were mainly xanthid crabs, *Sphaerocius* sp. and *Porcellana* sp.

Laboratory experiments on food preference showed that the smaller-sized *Sepiella inermis* fed chiefly on *Poecilia reticulata,* with one *Acetes* sp. eaten by one of the 2 cuttlefish (Table 4). The larger cuttlefish showed a preference for *P. reticulata,* but they also fed on *Acetes* sp. and *Dotilla* sp., which were eaten in almost equal numbers.

In the experiment on size selectivity, *Sepiella inermis* of the 15 to 20 mm size class chose only the smaller prey (Table 5). Each of the 3 cuttlefish took only 3 fish which is probably their feeding capacity for prey about 10 mm in length. When a pure offer of 30 mm prey was presented only one fish was taken per meal. It would appear, therefore, that when choice is available, as in the mixed offer, the smaller *S. inermis* exhibited a definite preference for smaller prey.

The larger *Sepiella inermis* do not show a distinct preference for any particular size of prey. In the mixed offer, both sizes of prey were eaten in almost equal numbers (Table 5).

Table 2

Monthly Feeding Intensity in Relation to Sex and Maturity

Types	Juveniles					Adult Males					Adult Females				
	Feeding Intensity				No. exam.	Feeding Intensity				No. exam.	Feeding Intensity				No. exam.
Month	H	F	S	E		H	F	S	E		H	F	S	E	
April	0	0	2	0	2	0	1	2	0	3	0	2	0	0	2
May	1	0	0	1	2	4	6	5	0	15	0	2	8	2	12
June	1	1	0	2	4	1	0	0	1	2	0	0	2	0	2
July	0	1	1	0	2	4	2	2	1	9	0	2	0	0	2
Aug.	–	–	–	–	–	4	1	3	0	8	1	2	1	0	4

H: Heavy feeding
F : Full stomach
S : Slight feeding
E : Empty stomach

Table 3

Percentage occurrence of Food Items in the Stomach of the Two Size Groups of *Sepiella inermis*

	< 25 cm Mantle Length				> 25 cm Mantle Length			
Size of cuttlefish	Number with different food type			No.	Number with different food type			No.
Month	Prawn	Fish	Crab	exam.	Prawn	Fish	Crab	exam.
April	2	0	0	2	4	10	0	14
May	2	0	0	2	9	18	5	26
June	2	0	0	2	9	4	0	9
July	3	0	0	3	9	4	0	11
August	–	–	–	–	5	5	0	9

Table 4

Number and Types of Prey Consumed in Half an Hour by the Two Size Groups of *Sepiella inermis* given a Mixed Offer of Ten Individuals of each Prey Type

Size of *Sepiella inermis*	Replicate Number	Prey Type *Poecilia reticulata*	*Acetes* sp.	*Dotilla* sp.
15 - 20 mm	1	2	1	0
	2	3	0	0
40 - 45 mm	1	6	2	1
	2	4	2	2

Acetes sp., are more easily captured than *Stolephorus*.

However, in the laboratory more fish than prawns were consumed by the juvenile predator, although both prey species appeared to be equally slow swimmers. This preference is probably due to the visual difference between the 2 types of prey. *Poecilia reticulata* are usually coloured and more opaque than the *Acetes,* which are more transparent. The former species is therefore probably more easily detected by *Sepiella inermis.* Illumination intensity in the laboratory may be higher than that in the sea and the transparent-looking *Acetes* under such conditions would probably be difficult to detect.

Table 5

Prey Size Preference by Two Size Groups of *Sepiella inermis* (ten prey individuals per size group were offered at any one time)

Size of *Sepiella inermis*	Replicate Number	No. of *Poecilia reticulata* consumed in $\frac{1}{2}$ hour: Mixed Offer 10 cm	Mixed Offer 30 cm	Pure Offer 10 cm	Pure Offer 30 cm
15 - 20 mm	1	4	0	2	1
	2	3	0	3	0
	3	3	0	3	1
40 - 45 mm	1	4	3	5	3
	2	3	3	5	5
	3	3	2	5	4

DISCUSSION

Boycott (1958) and Wells (1962) have suggested that young *Sepia officinalis* feed instinctively on mysids; then they learn to feed on other prey as they grow older. This is probably not the reason why only *Acetes* sp. were found in the stomachs of juvenile *Sepiella inermis.* Since laboratory experiments showed that juvenile *S. inermis* can feed on prey other than prawns, it indicates that *Acetes* consumption in the natural environment is not governed by instinct alone, but rather by the ease of capture of the prey. In the natural environment juvenile cuttlefish were probably unable to capture the larger and faster swimming prey, such as *Stolephorus* sp. The preference for smaller *Poecilia reticulata* in the laboratory experiment also indicates the relative inability of smaller *S. inermis* to capture larger and faster swimming prey. Thus, in the natural environment smaller and slower swimming prey, such as

Adult *Sepiella inermis,* on the other hand, feed on both *Stolephorus* and *Acetes* in the natural environment. They are faster swimming and therefore able to capture the faster swimming prey, such as the *Stolephorus* sp.

Both *Stolephorus* and *Acetes* are available in the seas around Singapore throughout the year, but their availability is generally low in May (Khoo, 1966). It is interesting to note that during this month crabs are also found in the diet of adult *Sepiella inermis.* These crabs are normally found on the "kelong" poles and are readily available. It would appear, therefore, that crabs are not eaten when the other food items, such as *Acetes* and *Stolephorus*, are abundant, but are only consumed when the latter food items are low in availability.

Laboratory observations also showed a selectivity against crabs. The crabs, using their pincers, threaten and discourage all but the biggest and most hungry cuttlefish.

The burrowing habits of the crabs may also make detection and capture difficult.

In conclusion, it appears that *Sepiella inermis* generally feeds on *Stolephorus* sp. and *Acetes* sp., with its feeding intensity and selectivity determined by the availability, the size, and the escape capability of the prey as well as the size and predatory response of the cuttlefish.

ACKNOWLEDGMENTS

We wish to thank Professor S. H. Chuang and the late Professor D. S. Johnson of the Zoology Department, University of Singapore, for all the help they have given.

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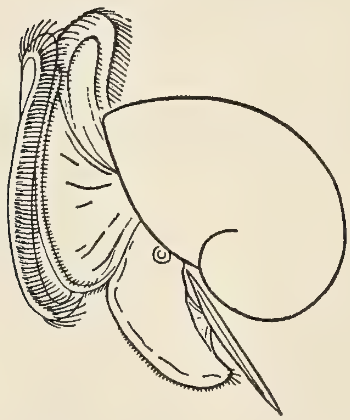

Some Notes on the Distribution and Taxonomy of Haliotids

(Mollusca : Gastropoda)

BY

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INTRODUCTION

RECENTLY WHILE rearranging some specimen trays filled with Haliotids, I noted several lots that in my opinion warranted a few brief notes on the distribution and taxonomy of this genus. Some of the specimens appeared to represent material from localities that would extend the published ranges of a species by only a few degrees of latitude or longitude, or both, while other collecting stations seemed to represent major extensions of such published range. A few specimens validated early records from definite localities, confirming identifications that at times had been questioned because of lack of comparative specimens in major research collections taken from such localities. The specimens discussed here were collected for the most part on the Thailand Coast of the Andaman Sea and at Trincomalee, Ceylon. The major part of the shells were obtained by Mr. George Mendenhall of San Bruno, California, and by my son, Robert C. Talmadge, now of Campbell, California.

In this study, identifications were made by direct comparison with homeotype specimens, that is, specimens that had been compared with the original type material and had been found to be the same species or subspecies. I have found that in some species of the Haliotidae there is no noticeable shell difference between populations extending over a rather wide geographical range, while in other species there may be several distinct geographical races or subspecies. All of this presents problems of identification, especially where there is a discontinuous distribution within the range of a species.

These notes are presented in the hope that they may be of some use to students of systematic malacology and perhaps to marine biologists working on spatial distribution.

SYSTEMATIC ACCOUNT

Haliotis Linnaeus, 1758

Type species: *Haliotis asinina* Linnaeus, 1758, by SD, MONTFORT, 1810, Conchyl. Systèm. 2: 119; Paris. Under "L'Haliotide" [*Haliotis asinina*], Montfort states "Espèce servant de type au genre." I quote this reference as there are several species utilized as the type of the genus in later publications.

(Haliotis s. s.)

Haliotis (Haliotis) asinina Linnaeus, 1758

Mr. George Mendenhall kindly allowed me to examine his series of Haliotids obtained from the shores of some small islands in the Andaman Sea off the west coast of Thailand. Mendenhall had obtained series of 3 species, among which was a suite of *Haliotis asinina,* which could not be separated by shell characteristics from any other population of the species that I had worked with. It appears that this widely distributed species is the same from the Ryukyu Islands in the north to Queensland in the south. Mendenhall's location, lat. 8°30′N; long. 98°00′ E, is north of Penang, off the west coast of the Malay Peninsula, my only record from this area.

(Padollus) Montfort, 1810

Type species *Haliotis parva* Linnaeus, 1758

Haliotis (Padollus) ovina Gmelin, 1791

To my locality records (TALMADGE, 1963), I can now add the Gulf of Siam (lat. 9°30′N; long. 100°00′E), Andaman Sea, Mendenhall collection, and a specimen from Quobba, Western Australia (lat. approx. 25°00′S). Although *Haliotis ovina* may be found with several color phases – brown, green, red and even yellow – these color variations may be and are found in any population, regardless of locality. So far as I can determine, it is impossible to separate populations on shell characteristics, nor does the species appear to have changed since Pliocene time.

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(Sanhaliotis) Iredale, 1929

Type species *Haliotis varia* Linnaeus, 1758

Haliotis (Sanhaliotis) varia Linnaeus, 1758

PILSBRY (1890) listed "Ceylon" along with many other localities from which this species was recorded. He included "Mozambique" and the "Red Sea", as well as the Indian Ocean island of Mauritius and island of Bourbon [= Réunion] within the range of the species. During the several years that I have studied the haliotids, I had never seen an authentic specimen of *Haliotis varia* from any of these localities. In the material available to me, and in the major research collections, all such material labeled as *H. varia* turned out to be *H. pustulata* Reeve, 1846. This last-named species does have variations, but at no time have I found these to match the population variations of *H. varia*. So it was with great surprise that I recognized *H. varia* in a series of haliotids taken by my son from a subtidal reef off Trincomalee, Ceylon.

In my previous work with this species (TALMADGE, 1962-1963) I had found that there was a rather broad separation of shell characteristics within the total range of the species. These variations could be separated into 3 geographical units, each with a definite center of distribution. There was no anatomical difference between Philippine, Indonesian, and Australian specimens, but there were shell characteristics that set these 3 races apart, not considering color and color patterns of the shell. Like *Haliotis ovina, H. varia* exhibits several color phases and patterns that cannot be associated with any particular local population.

Based upon shell characters alone, the Trincomalee specimens appeared to be more closely related to the population of *Haliotis varia* in the central and southern Philippine Islands than to specimens in central and southern Indonesia, to *H. varia stomataeformis* Reeve, or to *H. varia aliena* Iredale from the northern coast of Australia. Actually the specimens fit into the nominate race, *H. varia varia*. This presents a problem of a split distribution pattern within a subspecies, and at this time I have no solution for it.

Haliotis (Sanhaliotis) pustulata Reeve, 1846

Two specimens of *Haliotis pustulata* were obtained at Trincomalee by my son, and this time the species was expected. PILSBRY (1890) has listed this species from Ceylon, and I had worked with material taken at several localities in the Persian Gulf and from East Africa. Specimens from Somaliland, the Red Sea and the Gulf of Suez and Aquaba differ in shell characters from the nominate population from more southern localities along the east African coast. The specimens that I had previously examined indicated that the nominate race, *H. pustulata pustulata* was the race from the Persian Gulf, and the Trincomalee specimens fell well within the range of variation of that subspecies. Again color could not be used for separation of the 2 races, but there is a noticeable difference in shell sculpture and shape between the 2 races (TALMADGE, 1971).

Haliotis (Sanhaliotis) planata Sowerby, 1883

This was perhaps the most common species noted in the Mendenhall material from the Andaman Sea, and the species was definitely the most common in the material collected on Ceylon. As far as I can determine there is no consistent separation of populations by shell characters into distinct geographical races or subspecies in this far-ranging haliotid. Such variations as do appear are only individual and are repeated in population after population with no regard to geographical regions. HAAS (1954) listed a rather large haliotid from Dubai in the Persian Gulf and identified it as this species, but he noted that the size and shape of the shell did not fulfill the requirements of *Haliotis planata*. All specimens of *Haliotis* that I have seen from this locality are *H. pustulata*, and the much larger, flat, strongly sculptured *H. maria* Gray has been collected nearby, also in the Persian Gulf.

These notes serve to indicate the need for additional material from the south of Asia. I doubt that haliotids are absent from many intermediate localities between the two widely separated regions, Ceylon and the Malay Peninsula, but the scattered records that are available are confusing. Careful field work probably will add to and clarify the distribution of most of these species.

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Epicaridium Larvae in *Mytilus californianus*

(Mollusca : Bivalvia)

BY

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(2 Text figures)

INTRODUCTION

A DESCRIPTION IS GIVEN of the epicaridium larvae (Isopoda, Epicaridea) found among the washings from the mantle cavity of *Mytilus californianus* Conrad, 1837. These larvae were discovered during a survey of the symbionts of *M. californianus.* This is the first report to my knowledge of an epicarid isopod being associated with a non-crustacean host.

MATERIAL AND METHODS

Examination of 124 mussels revealed the presence of epicarid larvae in only 2 mussels, 5 from one and 13 from another. They have the characteristic form of the first larval stage (epicaridium) of the isopodan suborder Epicaridea. All of the mussels examined were collected from the high intertidal zone at Windmill Beach on Bodega Head, Sonoma County, California.

The larvae were mounted in Turtox mounting medium CMC10 and CMCS.

All figures were drawn with the aid of a camera lucida.

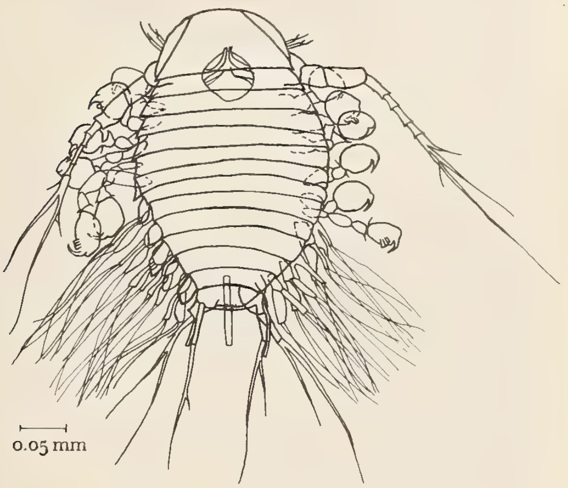

Figure 1

Epicaridium larva found in *Mytilus californianus*

DESCRIPTION OF THE EPICARIDIUM LARVA

Body strongly convex dorsally, with 7 free thoracic segments and 6 free abdominal segments. Average length of 11 larvae: 0.40 mm (0.32 - 0.67 mm); average width 0.23 mm (0.18 - 0.31 mm). Body length approximately 1.7 times its width.

Head large. Length of cephalon approximately $\frac{1}{4}$ its width.

Eyes absent.

Antennules (1^{st} antennae) biramous, with one ramus twice as long as the other. Longer ramus comprised of 2 articles. Two setae, one twice as long as the other, project from the tip of each ramus.

Antennae (2^{nd} antennae) long, extending to $\frac{1}{3}$ the length of uropods, about 13 times the length of antenna 1. Peduncle with 3 articles, flagellum with 5 articles. Each flagellum terminates in 3 fine setae, probably sensory in function. Seta 1 half as long at seta 2, which is half as long as seta 3.

Mouthparts (Figure 2C) difficult to interpret. Slender mandibles form a forward-directed tube which suggests that they are capable of piercing and sucking.

All 6 pairs of peraeopods (Figure 2A) strongly prehensile with long, curved dactylus closing against a large, subovate propodus. Carina present on posterolateral margin of each propodus. Anterior and posterior lateral margins at distal end of carpus each bear one spine.

Coxal plates become progressively larger posteriorly.

Five pairs of biramous pleopods (Figure 2B) present. One ramus of each natatory pleopod with 2 lateral setae. Second ramus with 3 lateral setae.

Uropods biramous. Endopod slightly longer than exopod. Both branches with 2 terminal setae.

Anal tube approximately as long as uropodal endopod.

DISCUSSION

The first larval stage of the epicarids is generally considered to be a component of the plankton, either free (when first released) or attached to copepods (CAULLERY, 1952: 69; SCHULTZ, 1969: 309; BAER, 1971: 59). In either case, one might expect to find a random distribution of larvae in filter feeders such as mussels, rather than clustered in 2 mussels. Moreover, the clustering phenomenon suggests that possibly other factors may be involved which account for the presence of these larvae in the mussels. The intertidal communities, of which the mussel beds are part, are composed of a number of potential hosts for epicarid isopods, and as a reproductive strategy, it could be advantageous for the newly hatched larvae to remain in the vicinity of their definitive hosts.

The epicaridium larva described in this paper cannot as yet be assigned to any particular adult epicarid isopod. Presently, I am surveying the epicarid isopods found at Bodega Head with the hope of describing their first larval stage. This study may reveal the identity of the epicaridium larvae found in *Mytilus californianus*.

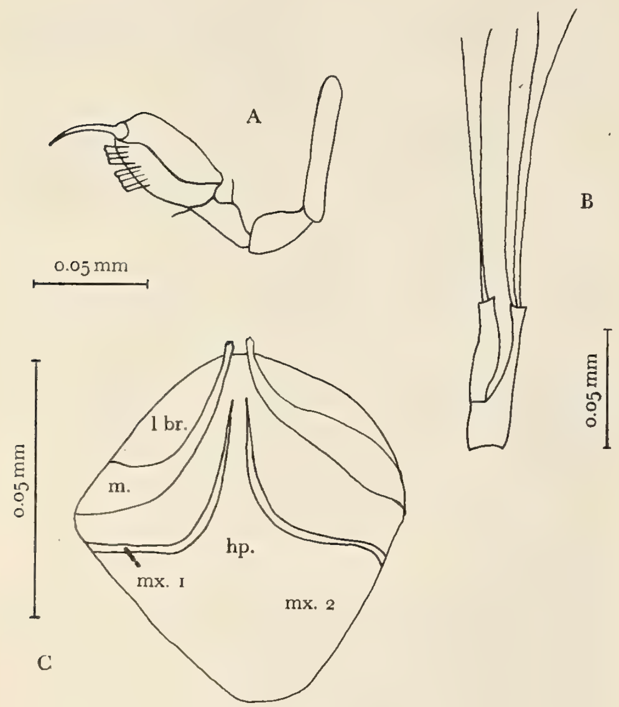

Figure 2

Epicaridium larva

A – peraeopod B – pleopod C – mouthparts: hp – hypopharynx lbr – labrum m – mandible mx. 1 – first maxilla mx. 2 – second maxilla

SUMMARY

A detailed description is given of the epicaridium larvae (Isopoda, Epicaridea) found among washings from the mantle cavity of *Mytilus californianus* (Mollusca, Bivalvia).

ACKNOWLEDGMENTS

I am grateful to Dr. Cadet Hand, Director of the University of California Bodega Marine Laboratory, for providing me facilities to work at the laboratory. I am indebted to both Dr. Milton A. Miller and Dr. Cadet Hand for critically reviewing the manuscript.

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Effects of Body Weight on Feeding and Radula Size in the Fresh Water Snail *Pila globosa*

BY

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(2 Text figures)

LAKE IDUMBAN KULAM (Palni, South India) is a permanent aquatic system covering an area of 666 100 m^2. The annual harvest from the fishery resources of this unmanaged natural pond is about 8 000 kg. The major producers in this system are *Chara* and *Hydrilla*, and *Ceratophyllum* (biomass: 661 g wet weight/m^2). A greater part of the plant energy is at present channeled via the most successful and abundant snail population, *Pila globosa* (Swainson, 1822) (biomass: 56 g/m^2). Since it is known that experimental determination of food intake and conversion efficiency may offer the most important clues in regard to ecological success of an organism (BRETT, 1970; KINNE, 1971), we have undertaken an extensive investigation to study the ecological energetics of *P. globosa* population with an ultimate view of eliminating it without disturbing other organisms from the ecosystem and thus make more plant energy available for the herbivorous fish populations.

Previous authors have reported the energy balance of a number of mollusks, *e. g.*, *Aplysia* (CAREFOOT, 1967), *Tegula* (PAINE, 1971) and *Scrobicularia* (HUGHES, 1969, 1970). Body weight is known to modify feeding rate and conversion efficiency (*e. g.*, PANDIAN, 1967; GERKING, 1971); however, the above mentioned authors have not given due consideration to the effect of body weight on energy balance of the respective mollusks and their estimates on rate and efficiency of energy transfer by these different molluscan populations may thus include an important source of error. This source of error has been eliminated in assessing ecological energetics of grasshopper populations (DELVI, 1972; see also DELVI & PANDIAN, 1972; PANDIAN & DELVI, 1974). The present paper, first of its series, deals with the effects of body size on the feeding rate of *Pila globosa* and also brings out a correlation between the feeding rate and radula weight with increasing body weight.

More than 100 individuals of *Pila globosa* of the weight range from 1 to 32 g (including the shell) were individually fed *ad libitum* on the natural food plant, *Ceratophyllum*, in the laboratory for a period of 30 to 40 days. Appropriate corrections were made for the amount of plant substance produced due to photosynthesis during the experimental period, in which the plant was fed in the test aquaria (capacity 2 l). The quantity of food consumed by the test individuals varied considerably; frequently, a day of intensive feeding was followed by a day of low feeding. Such day-to-day fluctuations have also been observed in fishes (*e. g.*, PANDIAN, 1967), and in grasshoppers (*e. g.*, DELVI & PANDIAN, 1972, 1973). On averaging the food quantity consumed during the test period (30 to 40 days), a certain trend became apparent. Feeding rate was 24.05 mg/dry plant/g live snail/day in an individual weighing 1 g. It decreased rapidly to about 13.07 mg/g/day for an individual of 4 g and then gradually to 2.12 mg/g/day for the largest animal tested (32 g) (Figure 1). Separate regressions were necessary to calculate the relationship between body weight and feeding rate; individuals weighing up to 4 g were considered under group 1, (the values obtained are indicated by ● in Figures 1 and 2), while those weighing from 4.1 to 24.0 g under group 2 (the values obtained are indicated by ○ in Figures 1 and 2), and those over 24 g under group 3 (the values obtained are indicated by □ in Figures 1 and 2). The regression coefficients were $Y = 23.36 - 2.79x$ for group 1, $Y = 12.54 - 0.43x$ for group 2, and $Y = 3.12 - 0.015x$ for group 3; *i. e.*, they show that for 1 g increase in body weight of the snail, the decrease in daily food intake was 2.79, 0.43, and 0.015 mg

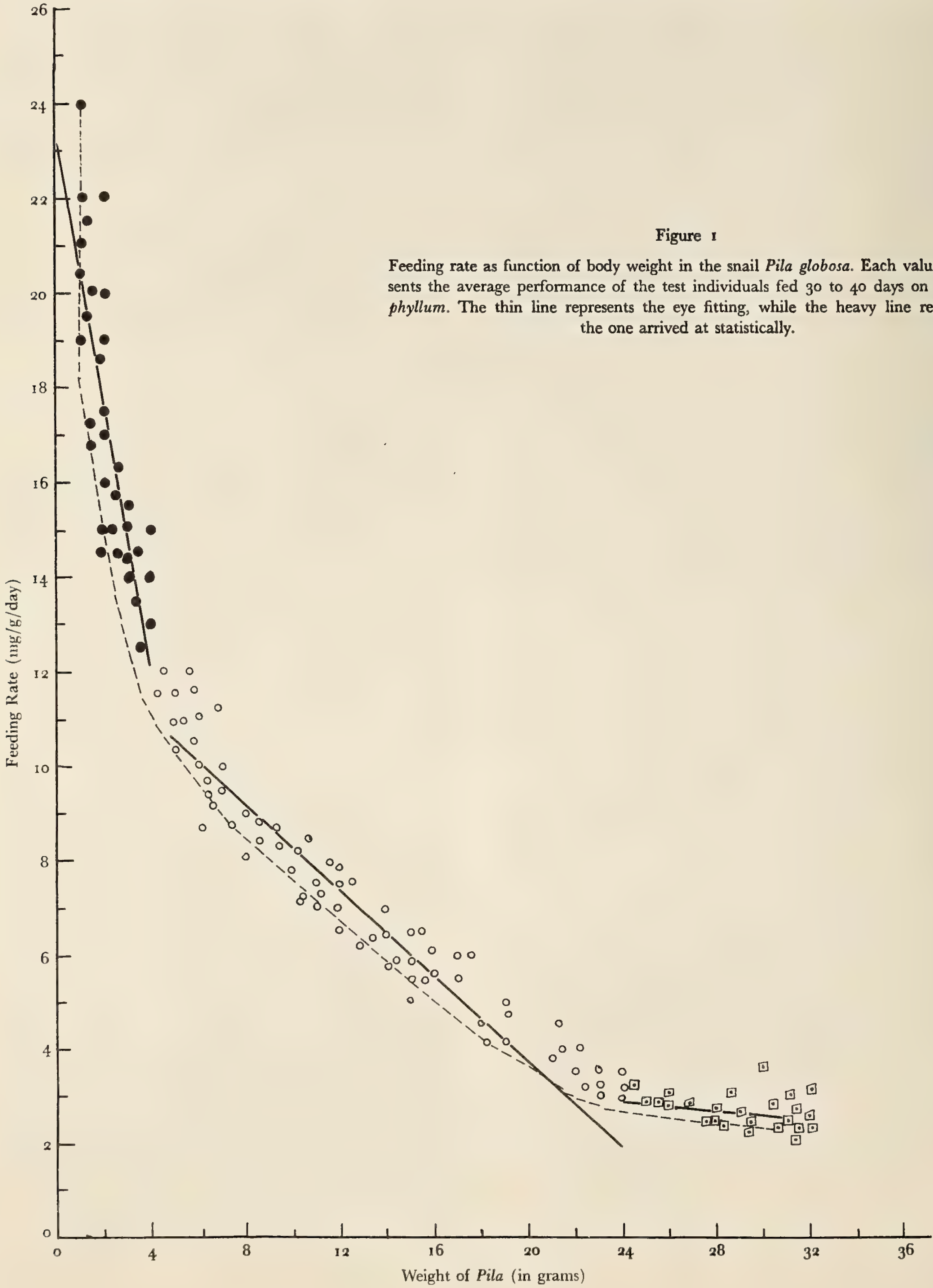

Figure 1

Feeding rate as function of body weight in the snail *Pila globosa*. Each value represents the average performance of the test individuals fed 30 to 40 days on *Ceratophyllum*. The thin line represents the eye fitting, while the heavy line represents the one arrived at statistically.

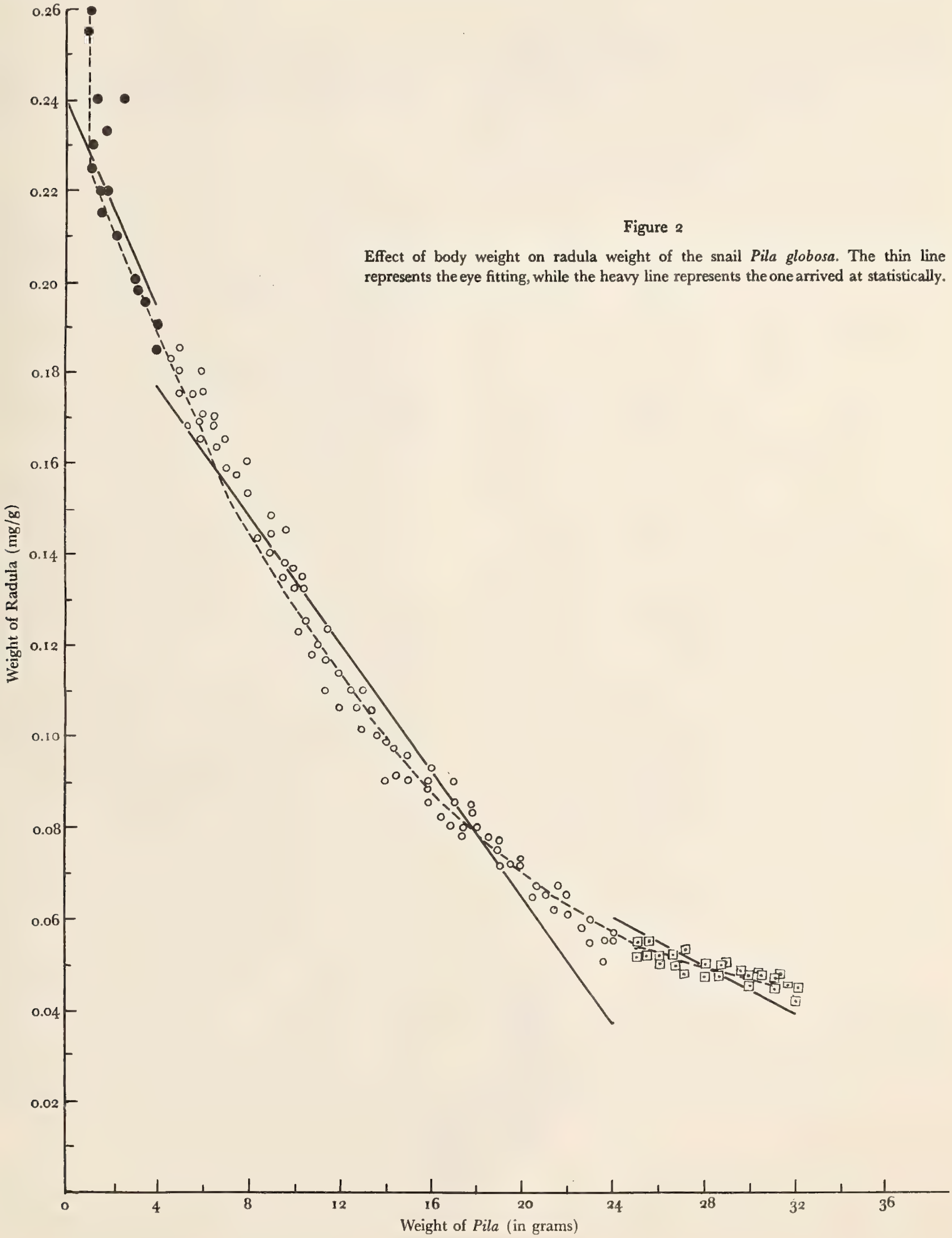

Figure 2

Effect of body weight on radula weight of the snail *Pila globosa*. The thin line represents the eye fitting, while the heavy line represents the one arrived at statistically.

dry plant among the individuals belonging to group 1, 2, and 3, respectively. The data reported for *Pila* fall within the range of values reported by previous workers. For instance, daily food intake of an individual weighing 24 g was 3.12 mg dry plant/g live animal. CAREFOOT (1970), who studied the effect of different algae on *Aplysia juliana* Quoy & Gaimard, 1832 (mean body weight 24 g), reported a series of values ranging from 0.85 mg dry *Cladophora* /g live *Aplysia*/day to 4.47 mg dry *Enteromorpha*/g live *Aplysia*/day.

It is well known that increase in body weight decreases metabolic level (ZEUTHEN, 1953; HEMMINGSEN, 1950, 1960) and hence feeding rate, a sensitive parameter of metabolism. The decrease in feeding rate may be associated with the phenomenon of ageing; ageing is known to operate via the deterioration in the condition of teeth, leading to digestive disturbances and malnutrition in herbivorous farm animals (BRODY, 1945). An attempt was made to know whether ageing operates also via deterioration and reduction of the teeth in the herbivorous snail *Pila globosa*. Figure 2 shows that there is a definite decrease of radula (dry) weight as the body weight of the snail increases and that the relation between body weight and radula weight is parallel to that observed for feeding rate-body weight relationships. The regression coefficients obtained were $Y = 0.249 - 0.0135x$ for group 1, $Y = 0.205 - 0.007x$ for group 2, and $Y = 0.118 - 0.0024x$ for group 3; *i. e.*, they show that for 1 g increase in body weight of the snail, the decrease in radula weight was 0.0135, 0.007, or 0.0024 mg dry weight among the individuals belonging to group 1, 2, or 3, respectively. Nevertheless, the trends obtained for the relationships are similar, though not identical. Therefore, decrease in radula weight *per se* is one of the important mechanisms through which body weight (or ageing) influences the feeding rate. Further work on enzyme activity and quantity as function of body weight is in progress.

ACKNOWLEDGMENTS

We are grateful to Professor Arunachalam for offering facilities, and to Mr. R. Baskaran for his help.

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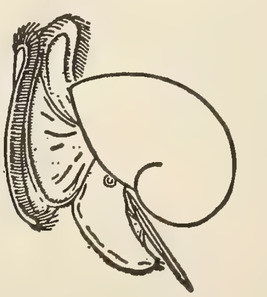

On the Possible Significance of Enhanced Glutamate Dehydrogenase Activity in Normal and Aestivated *Pila globosa*

BY

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(3 Text figures)

INTRODUCTION

ACTIVE LIFE OF THE SNAIL, *Pila globosa* (Swainson, 1822), is interrupted at intervals, during drought conditions, by aestivation during which the animal enters into a state of metabolic dormancy (MEENAKSHI, 1956a; GARTEN, 1958; RAGHUPATHIRAMI REDDY, 1965). During aestivation there is a decrease in the activities of Krebs cycle enzymes and the animal survives by anaerobic glycolysis utilizing slowly the glycogen reserve (SLATER, 1928; VON BRAND, BAERNSTEIN & MEHLMAN, 1950; MEHLMAN & VON BRAND, 1951, 1953; VON BRAND, MCMAHON & NOLAN, 1955; MEENAKSHI, 1956a, 1957; and REDDY, *op. cit.*). The glutamate level was found to increase in the soft parts of the aestivating snail, which was suggested to be of significance during aestivation (MURALI MOHAN, 1973; MURALI MOHAN *et al.*, 1973; RAMANA RAO, 1973). However, very little information is available regarding its specific involvement in the aestivation metabolism of *Pila globosa*. JANSSENS (1964) pointed out that "during aestivation there would be changes in the intermediary metabolism of great interest to the comparative biochemist but these have as yet been the subject of little experimental investigation." An attempt is made here to study the activity pattern of glutamate dehydrogenase during aestivation.

MATERIALS AND METHODS

Pila globosa were collected from the local fresh-water ponds and were maintained in aquaria for a week by feeding them on *Hydrilla* plants. Actively feeding snails were aestivated by embedding them in dry sand for different periods as required.

A 10% (w/v) homogenate of the hepatopancreas of normal and aestivated snails were prepared in 0.25 M sucrose in a chilled glass homogenizer. The homogenates were centrifuged at 4000 rpm and the supernatant was assayed for the enzyme activity.

The glutamate dehydrogenase (EC 1.4.1.3) was studied by the dye-reduction method (SRIKANTHAN & KRISHNAMURTHY, 1955) as modified by GOVINDAPPA & SWAMI (1965) using 2-(p-Idophenyl)-3-(p-nitrophenyl)-5-phenyl tetrazolium chloride (INT) (Koch-Light Laboratories Ltd., England) as the terminal electron acceptor. The assay mixture consisted of 50 μmoles of glutamate (BDH), 100 μmoles of phosphate buffer (pH 7.4), 4 μmoles of INT and 0.1 μmoles of NAD (E. Merck) in a final volume of 3 ml. The reduced formazon was extracted with 5 ml of toluene and the optical density was measured at 495 μm with Hilger & Watts U. V. Speck. Protein levels were estimated by the method of LOWRY *et al.* (1951). The

hepatopancreas isolated for the determination of water content was blotted gently on Watmann No. 1 filter paper and weighed. The tissues were kept in a hot-air oven at 100° C for 48 hours and the dry weight was determined.

RESULTS AND DISCUSSION

MEENAKSHI (1956a, 1964) reported no significant changes in the water content of the tissues in active and 6-months aestivated snails and these results agree with the present findings (Figure 1). MEENAKSHI (1956b) reported protein utilization in the aestivated snail, *Pila virens*. The protein levels in our findings have shown a decrease from the second month of aestivation, agreeing with the results of Meenakshi (Figure 2).

Changes in the enzyme activities in general during aestivation and hibernation in molluscs were reported (BALDWIN, 1938; CZAPSKA, 1959; ECKSTEIN & ABRAHAM, 1959; CHAFFE *et al.*, 1961; ANJANIPRASAD & KRISHNAMURTHY, 1962; BRYANT *et al.*, 1964; R. REDDY, 1964, 1965; MOHAN & DASS, 1969; RAO, 1973; S. REDDY, 1973). R. REDDY (1965) has reported a general decrease in the activity of glutamate dehydrogenase along with the alcohol and succinate dehydrogenases and other respiratory

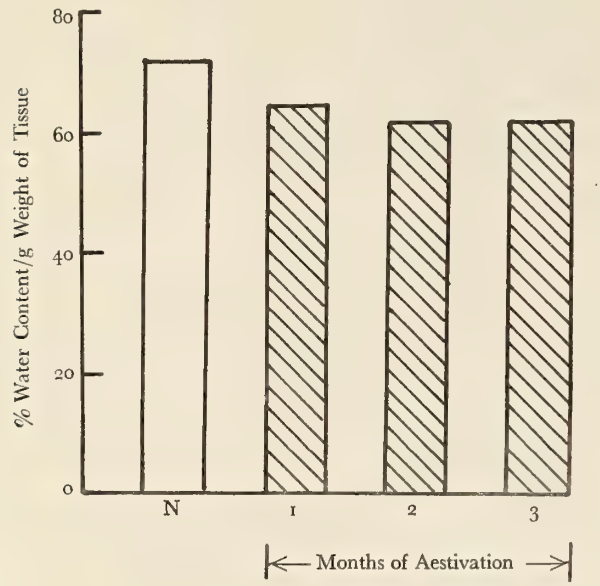

Figure 1

Water Content in the Normal and Aestivated *Pila globosa* (lined histograms represent the aestivated condition)

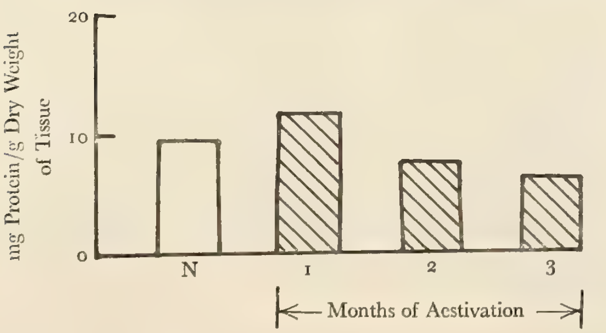

Figure 2

Protein Content in the Normal and Aestivated *Pila globosa* (lined histograms represent the aestivated condition)

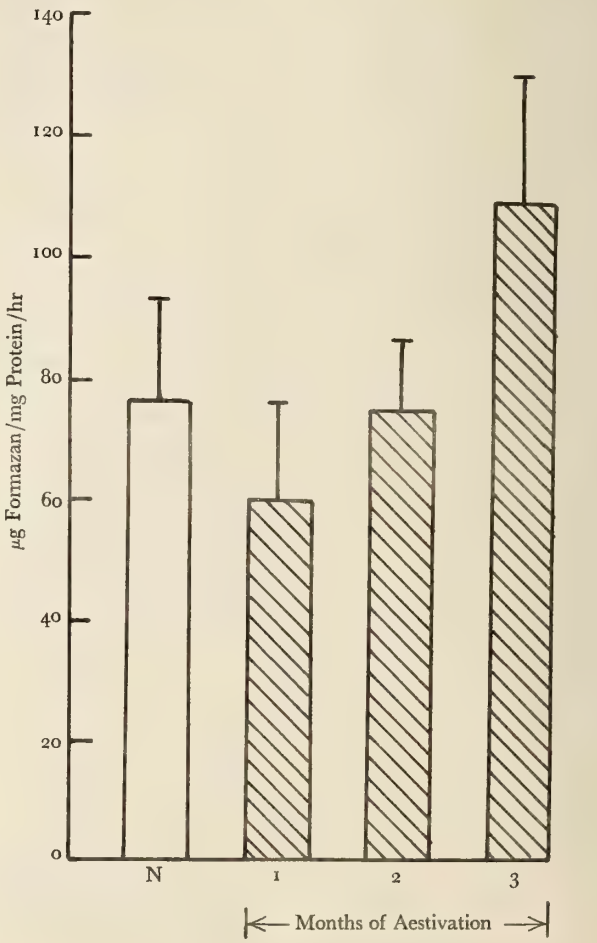

Figure 3

Glutamate Dehydrogenase Activity in the Normal and Aestivated *Pila globosa* (lined histograms represent the aestivated condition)

enzymes during aestivation. In contrast to the above findings, it has been observed in the present investigation that glutamate dehydrogenase shows a peculiar behaviour during aestivation. The activity levels decreased in the first month of aestivation which is in agreement with the results of R. REDDY (1965). But with prolonged periods of aestivation the activity showed a general increase over the normal level (Figure 3).

MEENAKSHI (1965b) reported protein utilization in the aestivated snail *Pila virens* and protein utilization normally leads to an increased ammonia level in the organism (FRUTON & SIMMONDS, 1960; HARPER, 1971). NAYEEMUNNISA (1972) reported decreased ammonia content in the mantle during aestivation. Results of S. REDDY (1973) were also in agreement with the results of Nayeemunnisa for the mantle, but in other tissues (foot, hepatopancreas and body fluids) the ammonia levels were constant during aestivation. Further, the works of the above cited authors, and of LAL & SAXENA (1952) and R. REDDY (1963) have shown increased uric acid content during aestivation in the soft parts of *Pila globosa*. The levels of aspartic acid and glutamic acid were found to increase in different tissues of the aestivating *P. globosa* (MOHAN, 1973; RAO, 1973). Under these physiological circumstances the glutamate dehydrogenase is expected to increase in the aestivation, as discussed below.

With the rise in the glutamate dehydrogenase activity, the ammonia produced by the protein utilization reacts with the endogenous α-ketoglutarate to form glutamate (HARPER, 1971). The glutamate thus formed may be metabolised in 2 ways, *viz.*, (1) by transamination and (2) by amidation. By transamination with oxaloacetic acid, aspartate is formed (MULLER & LEUTHARDT, 1950; HARPER, 1971; MAHLER & CORDES, 1969). The aspartate thus formed would be the source for nitrogen 1 of the purine ring and fumaric acid is the by-product (HARPER, *op. cit.*; LONG, 1961; MAHLER & CORDES, *op. cit.*). Fumaric acid is converted into oxaloacetic acid through the Krebs cycle enzymes (HARPER, *op. cit.*; LONG, *op. cit.*; MAHLER & CORDES, *op. cit.*). During transamination it is interesting to observe that α-ketoglutarate is also formed (MULLER & LEUTHARDT, *op. cit.*) Thus, it is likely that this regeneration of α-ketoglutarate and oxaloacetic acid may act as a compensatory mechanism and as a contributory factor for their maintenance at a constant level during aestivation, wherein the oxidative metabolism is avoided in favour of glycolysis (MEENAKSHI, 1956a). The second path for the glutamate utilization is by amidation to glutamine with ammonia (MAHLER & CORDES, *op. cit.*; HARPER, *op. cit.*), which supplies nitrogen atoms 3 and 9 of the purine ring and the by-product being glutamic acid (LONG, *op. cit.*; MAHLER & CORDES, *op. cit.*; HARPER, *op. cit.*). This may be the reason for the increased glutamate content of the hepatopancreas in the aestivating snail. Hepatopancreas being the site for uric acid biosynthesis (LAL & SAXENA, 1952), increased xanthine dehydrogenase activity was also reported during aestivation (S. REDDY, 1973). The aspartate and glutamate thus formed may constitute the precursors for the uric acid biosynthesis. Further investigations are being carried out in this laboratory to ascertain the exact role of aspartic and glutamic acids in the aestivation metabolism of *Pila globosa*.

SUMMARY

1. Water content, protein levels and levels of glutamate dehydrogenase activity were estimated in the hepatopancreas of normal and aestivated *Pila globosa*.
2. No significant loss of water content was observed. Protein levels were found to decrease.
3. Glutamate dehydrogenase activity was observed to increase in the aestivated *Pila globosa*, except in the first month.
4. These results were correlated with the increased uric acid biosynthesis.

ACKNOWLEDGMENT

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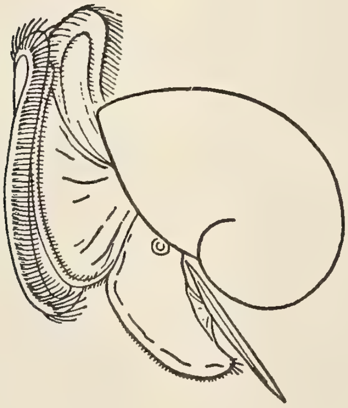

NOTES & NEWS

Soviet Contributions to Malacology in 1972

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THE MOLLUSCAN LITERATURE of the Soviet Union and its Eastern satellites constitutes a body of research frequently overlooked but immediately germane to many Western investigators. With a significant commitment to the study of the marine environment, the Russians have a number of publications which deal with aspects of biological oceanography. Noteworthy are those in which malacological contributions occur with some frequency: Izvestiia Tikhookeanskogo nauchnogo instituta rybnogo koziaistva i okeanografii (Transactions of the Pacific Research Institute of Fisheries and Oceanography) issued from Vladivostok; Trudy Atlanticheskii naucho-issledovatel'skii institut rybnogo khoziaistva i okeanografii (Works of the Atlantic Research Institute of Fisheries and Oceanography) published in Kaliningrad, and Issledovaniia fauny morei (Investigations on the fauna of the sea) from the Zoological Institute in Leningrad. Special institutes and series deal with the Azov, Black, White, and Caspian Seas, and during 1972 some explorations were carried on in the Red and the Davis sea in Antarctica.

Localized journals, the standard museum serials, and the publications of various societies of natural history deal with the land and freshwater faunas of the USSR.

Most experimental studies which are abstracted deal with the results of research in neurophysiology.

We have reviewed and translated the titles of pertinent Soviet literature abstracted by the Referativnyy Zhurnal during the year 1972. This abstracting service is a publication of the Government Committee of the Soviet Ministry of the USSR for Science and Technology (Gosudarstvennyy komitet soveta ministrov SSSR po nauke i tekhnike) and the Academy of Science (Akademiya nauk soyuza sovetskikh sotsialisticheskikh respublik) and is issued monthly in Moscow by the All Union Institute for Scientific and Technological Information (Vsesoyuznyy institut nauchnoy i teknicheskoy informatsii). Section D in Biology considers General Zoology, Invertebrate Zoology and Hydrobiology. The neontological literature on mollusks is listed under Invertebrate Zoology. Previously we have listed abstracts for the years 1968 to 1971 (Boss, 1969, The Veliger 12: 226 - 227; Boss & Jacobson, 1971, 1972, 1973, *ibid.*, 13: 199 - 202; 14: 437 - 440; 15: 362 to 366).

Abbreviations and symbols we have used are:

ES – English Summary
TAN – Trudy Atlanticheskii nauchno-issledovatel'skii institut rybnogo khoziaistva i okeanografii (Works of the Atlantic Research Institute of Fisheries and Oceanography)
ZEBP – Zhurnal Evolyutsionnoi biokhimii i Fiziologii (Journal of evolutionary biochemistry and physiology)
ZZ – Zoologicheskii Zhurnal (Zoological Journal)

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Re *Laura* Trinchese, 1872

(Gastropoda : Opisthobranchia)

BY

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IN A RECENT NOTE (KEEN, 1973), I showed that the earliest establishment of the generic name *Laura* in Mollusca is by Trinchese, 1872, rather than Trinchese, 1873 or 1874, as often cited. I was, of course, aware that there is listed in the nomenclators another (apparently later) usage of the name – "*Laura* Lacaze-Duthiers, 1883." I saw no reason to inquire further into the status of the latter. However, an alert correspondent, Gary MacDonald, soon called to my attention the fact that it is the basis for a family-group name, Lauridae, in ascothoracican barnacles, and that it is well embedded in cirriped literature. I then made further investigations, especially after noting that NEWMAN, ZULLO, & WITHERS (1969: R274) cite the date of *Laura* Lacaze-Duthiers as 1866, though they give no bibliographic reference. My intention was to ask the International Commission on Zoological Nomenclature to suppress the molluscan *Laura* (which, after all, has had little currency) in favor of the arthropod *Laura* if the 1866 date of the latter could not be confirmed. It is now evident that a request for suppression is not necessary: the barnacle *Laura* does have priority. It was validated in 1865 in a paper overlooked by compilers of the two principal nomenclators [NEAVE, "Nomenclator Zoologicus ..." and SCHULZE, KÜKENTHAL, & HEIDER, "Nomenclator animalium generum ..."]. Not only was the generic name proposed at that time, but a type species, *Laura gerardiae*, was named and described. [This is a cirriped parasitic on an antipatharian coral, *Gerardia*.]

The result for opisthobranch nomenclature is that *Placida* Trinchese, 1876, again becomes available, and *Laura* Trinchese, 1872, being a homonym, falls into synonymy under *Placida*.

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Geographic Displacement as a Non-Range-Extension of *Tegula gallina* (Forbes)

(Gastropoda : Trochidae)

BY

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ON 9 AUGUST 1973, 1410 dead and cleaned shells of the turban snail *Tegula gallina* (Forbes, 1852) were placed in a small area of the exposed rocky mid-intertidal zone, immediately northeast of the University of California Bodega Marine Laboratory, near Horseshoe Cove, Bodega Bay, Sonoma County, California for the purpose of studying aspects of hermit crab biology and ecology. Before

release, each shell was presented to and subsequently occupied by a hermit crab (*Pagurus samuelis* (Stimpson, 1857) and *P. hirsutiusculus* (Dana, 1851)) removed from shells of *Tegula funebralis* (A. Adams, 1855) collected from the same area. The *T. gallina* were collected living from the rocky intertidal zone at Flat Rock Point, Palos Verdes Peninsula, Los Angeles County, California. The snails (as well as all shell epizoics) were killed by boiling and the animals removed; no living *T. gallina,* which ranges from Santa Barbara County, California to Magdalena Bay, Baja California, were released at Bodega Bay. The study will be completed when no further shells of *T. gallina* can be recovered from the area.

In the unlikely event that any *Tegula gallina* should be recovered in the Bodega Bay area or adjacent regions through collecting (which is unlawful in the site of placement, a marine life refuge), such specimens are not to be regarded as indicating a range extension.

Two Symbioses of *Conus*

(Mollusca : Gastropoda)

with Brachyuran Crabs

BY

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(2 Text figures)

Conus californicus Reeve, 1844 can now be added to the long list of hosts of the brachygnathous decapod, *Opisthopus transversus* Rathbun, 1893, compiled by Beondé (1968). Ninety *C. californicus,* the greater part of a group aggregated around a massive cluster of *Conus* egg capsules, were collected at a depth of 33 m in Sumner Canyon off La Jolla, California, on 5 July 1972 and preserved in 70% ethanol. In examining the soft parts of these cones, I discovered 9 crabs, each securely lodged under the mantle of a *Conus,* behind the ctenidium (Figure 1). These were identified by Janet Haig of the Allan Hancock Foundation as juveniles of the pinnotherid *O. transversus.*

Within the mantle cavity, the crabs faced either toward or away from the anterior canal, clinging closely to the body of the cone, but without piercing the underlying tissue. The basic color, a lustrous creamy beige, was overlain on the carapace by a reticulation of fine, punctate, orange lines. This bright pattern, which was visible through the mantle and first drew my attention to the presence of the pinnotherids, has gradually disappeared.

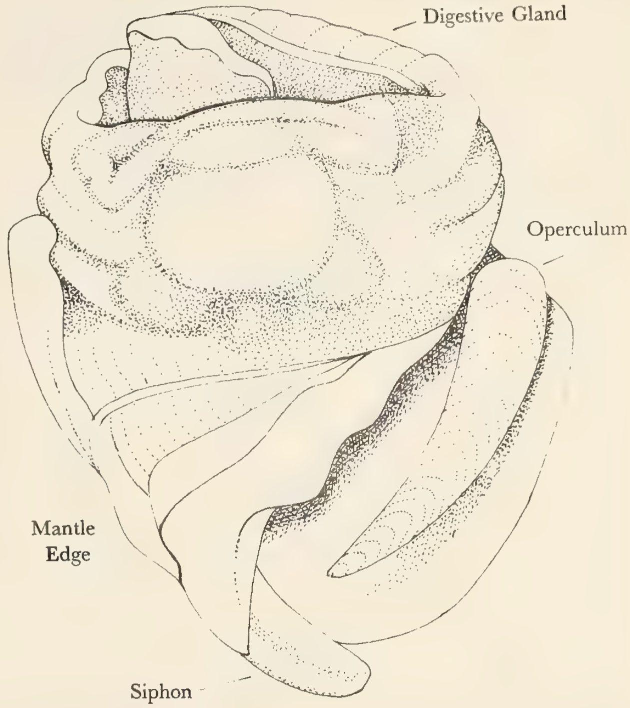

Figure 1

Conus californicus removed from shell, showing a specimen of *Opisthopus transversus* under the mantle

In 81 *Conus californicus* from several intertidal collections in the San Diego area, I found only one *Opisthopus transversus*: a small individual occupying one of 37 cones taken in the Flood Control Channel in January 1965. Its appendages are a light cream color, carapace and abdomen are a solid rust-red; the mottling which Hopkins & Scanland (1964) describe as characteristic of very young *O. transversus* is lacking.

Data for both "guests" and hosts are given in Table 1. Due to shrinkage of the molluscan body in the preservative, the often unavoidable destruction of tissue in removing the cone from its shell, and occasional loss of appendages in releasing the crab from the mantle cavity, the

Table 1

Sexes and approximate maximum dimensions of the symbiotic pairs of *Conus californicus* and *Opisthopus transversus,* with displacement volumes and percent of cone body volume occupied by the crab

Conus californicus						*Opisthopus transversus*					
	Shell		Body				Carapace			Total	% of *Conus* body occupied
Sex	Width mm	Length mm	Width mm	Length mm	Volume cm^3	Sex	Breadth mm	Width mm	Length mm	Volume cm^3	
from Sumner Canyon											
♀	14	23	9	13	0.30 [1]	♂	1.5	4.5	3.5	0.14	[1]
♂	14	24	10	14.5	0.49	♂	2	4.5	4	0.14	28.6
♂	15	25	10	13	0.60	♂	1.5	4.0	3.5	0.10	16.7
♀	15	26	10	14	0.59	♂	1.5	5.0	4.5	0.14	23.7
♀	16	27	10	15	0.60	♂	2	5.5	4.5	0.19	32.8
♀	16	28	12.5	15	1.12	♂	2.5	4.5	4.0	0.15	13.4
♂	16	28	12.5	16	0.63	♂	2	5.0	4.5	0.09	14.3
♀	18	30	12	18	1.4	♂	2	5.0	4.5	0.18	12.8
♀	18	31	12	20	0.91	♂	2	6.0	4.5	0.16	17.6
from Flood Control Channel											
♀	13	22	8.5	13	0.47	♂	1	3.5	3	0.17	31.9
											$\overline{X}=21.31$

[1] damaged, tissue missing

volume measurements are lower than they would have been *in vivo.* Nevertheless, the values presented provide a rough estimation of the space available to the crabs, the percentage of that space which they occupy, and the relative sizes of the partners.

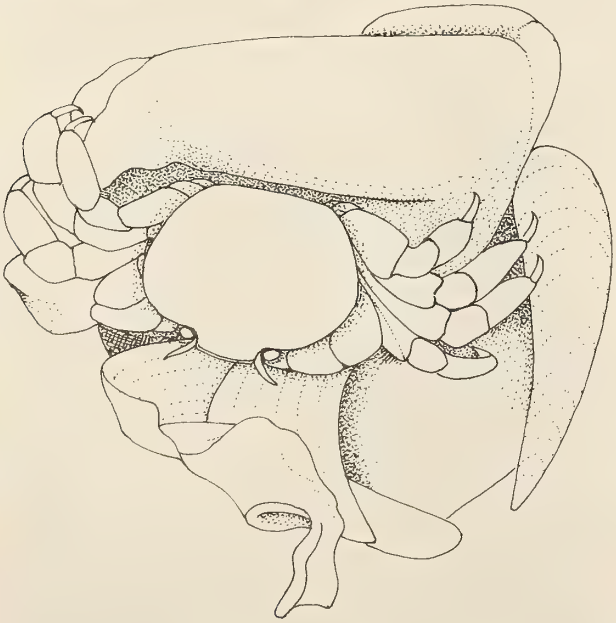

Figure 2

Opisthopus transversus in situ in mantle cavity of *Conus californicus* (mantle reflected)

To date I have looked for similar relationships in 4 Panamic species of *Conus.* No crabs were found in 81 *C. perplexus* Sowerby, 1857 and 12 *C. regularis* Sowerby, 1833, taken intertidally near San Felipe, Baja California, Mexico, in early June 1973. On 30 November 1972, I collected 32 *C. nux* Broderip, 1833 and 11 *C. purpurascens* Sowerby, 1833, while diving at La Palmilla on the southeast coast of the Gulf of California. There were no symbionts with the *C. nux.* However, 3 crabs were found in the container to which the bodies of 10 of the *C. purpurascens* had been removed, and when the body of the 11th *C. purpurascens* was extracted from its shell, a 4th crab came with it. There was no evidence on the bodies of the cones, such as the impress that *Opisthopus* had left on the *C. californicus,* that these crabs assume a position under the mantle; the relationship in this case must consist in the crab sheltering within the shell, maintaining a position peripheral to, rather than within, the body of the cone.

These crabs have been identified by Janet Haig as *Mithrax (Mithraculus) denticulatus* Bell, spider crabs of the family Majidae. Ms. Haig informs me that the genus is usually free-living, but that *M. denticulatus* has been reported to hide in corals. A recently described Caribbean species, *M. commensalis,* is apparently symbiotic with an anthozoan (MANNING, 1970).

The carapace of *Mithrax denticulatus* forms a triangle of equal base and height; maxima for these dimensions for the 3 specimens that could have been associated with any of the 10 *Conus purpurascens* placed in a common con-

tainer are 4.5, 5 and 12 mm; shell sizes for the 10 cones range from 17×26 mm to 30×49 mm. The 4th crab measures 5 mm, and was definitely associated with a cone measuring 30×51 mm. The predominant orange color of the spider crabs is also fading.

Several salient features emerge from the information presented:

1. The relationship of *Opisthopus transversus* to its numerous hosts is usually described as commensal and, in several cases, the crab is known to rely on the host's feeding for its food supply (BEONDÉ, 1968; HOPKINS & SCANLAND, 1964). It seems unlikely that *Opisthopus* can gain this advantage in a carnivorous species, such as *Conus californicus,* whose food is taken into the buccal cavity and processed internally (SAUNDERS & WOLFSON, 1961). Unless sufficient nutrients are carried to it by the gastropod's pallial current, it seems that *O. transversus* must leave the cone, as BEONDÉ (*op. cit.*) postulates it leaves *Aplysia,* to forage. Furthermore, HOPKINS & SCANLAND (*op. cit.*) suggest that *O. transversus* inhabiting *Astraea, Bulla* and *Megathura* procures its own food.

2. HOPKINS & SCANLAND (1964) relate variations in color pattern in *Opisthopus* to the feeding type of the particular host. This suggestion cannot pertain here; although inhabiting the same host species, there is a striking difference between the solid-red carapace of the *Opisthopus* in the intertidal *Conus californicus* and the delicately patterned carapaces of the crabs from the subtidal cones. However, it appears that both method of preservation and lapse of time between collection and examination must be considered in comparing color patterns.

3. In both of these associations with *Conus,* the "guest" occupies a considerable portion of the host's volume. *Opisthopus transversus* appropriates, on the average, $\frac{1}{8}$ of the volume of *C. californicus.* In the *Conus-Mithrax* association, which probably involves the sheltering of the crab within the cone shell for periods of variable duration, cohabitation by any of the 3 smaller spider crabs with even the smallest of the *C. purpurascens* would not appear to be restrictive to either animal. Unfortunately, it cannot be established which of the 10 cones whose bodies were placed in a single container actually harbored the large *M. denticulatus.* The most conservative case, in terms of relative volume occupied by each partner, would be for it to pair with the largest of the 10 cones. Displacement volumes are 0.6 cm^3 for the large *Mithrax* and 2.56 cm^3 for the body of the large cone; internal volume of the cone shell (determined as the amount of liquid the empty shell will hold) is 4.0 cm^3. Thus, the gastropod's body would fill 64% of the shell and the crab an additional 15%. Since these calculations disregard both shrinkage of the preserved molluscan body and the extra volume the living crab would occupy in its normal movements, less than 20% would remain as extra-corporeal space. The combination of the second-largest *C. purpurascens* and the large *Mithrax* would leave less than 5%. Possible adverse effects of these spacial relationships warrant consideration in defining the type of symbiosis.

4. Sex ratios of both partners to these symbioses are unbalanced. Eight of the 11 *Conus purpurascens* are males; 3 of the *Mithrax* are males; the 4th, which is considerably larger, is the only female of the 14 crustaceans involved. While the sex ratio of the total sample of 90 subtidal *Conus californicus* is 35 males to 55 females, 7 of the 9 specimens occupied by *Opisthopus* are males. Most strikingly, all of the *Opisthopus* are males; the probability that such a sample would be collected by chance from a population in which equal numbers of male and female *O. transversus* occupied *C. californicus* is less than 1 in 200.

5. HOPKINS & SCANLAND (1964) conclude that the size of the host cavity occupied by *Opisthopus transversus* limits the size which the crab can attain while being party to the relationship. Furthermore, Scanland reports (personal communication) that the largest female *O. transversus* in any of the hosts he has examined measured 1 cm in carapace width, and suggests that protandry may be involved. In view of the fact that the *O. transversus* reported here are all juvenile males, the possibility that this symbiosis occurs only during one phase in the life cycle of the pinnotherid is another aspect of the relationship which merits investigation.

ACKNOWLEDGMENTS

George Lewbel and Dr. Arthur Wolfson of Scripps Institution of Oceanography collected the subtidal *Conus* and tendered advice. The *C. perplexus* and *C. regularis* were collected by David Mulliner and family. Anthony D'Attilio of the San Diego Natural History Museum drew the figures.

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Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

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The publication date of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Post Office does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

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In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

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It is general knowledge that in spite of the optimistic statements made in the propaganda disseminated by the U. S. Postal Service, the service continues to deteriorate. Regrettably, however, the United States of America is not alone in this respect. Evidence is accumulating in our offices to the effect that irregularities occur in other countries as well; to our surprise, Japan is one of these. Since we have designed a system which makes it impossible to omit mailing copies of our journal to any member or subscriber who is paid up, and because of the regulations pertaining to the second class mailing permits, we know that if a copy does not reach the addressee, the fault lies with the postal system of the country or area of destination. Our complaints to the local Post Office can bear no fruit in such cases. We must request our members and subscribers to inquire at their local post offices if their copies do not arrive. We cannot replace lost copies free of charge and, unless the journal were mailed by insured post, the Post Office will not indemnify the injured party. The losses we have sustained in the past years have been mounting steadily, and not in proportion to our increased circulation.

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We must call the attention of our Members and Subscribers to the fact that we mail our journal on the date stated on the cover of a particular issue. After we have delivered the journal to the Post Office, our control ends. Delays in delivery seem to become more and more common. Needless to say that we regret this very much; we had hoped that when the salaries of the Postal Workers were increased, the service would improve. However, this seems not to be the case.

Late News

If the address sheet of this issue is **PINK**, it is to indicate that **your** dues remittance had not arrived at the time the mailing was prepared (*i. e.,* by March 1, 1974). We wish to take this opportunity to remind our Members that a reinstatement fee of one dollar becomes due if membership renewals have not been received by C. M. S., Inc. by April 15, 1974. However, in view of the extremely slow postal service, members should not be alarmed by this notice as their remittances may be received between the first of March and the date of mailing this issue. Surface mail in the United States may take several weeks - there is no longer any air-lift program; from overseas addresses we must allow a minimum of 6 weeks for surface mail.

The **pink sheet** is intended only as a reminder and we resort to this means to save on postage charges.

—→ As we go to press, we learn that postage rates on various classes of mail, both domestic and foreign, will be increased substantially. However, we are unable to learn exactly how much the increases will be. We will, therefore, maintain the presently announced rates and handling charges until July 1, 1974. At that time we will announce our revised schedules. Membership dues and subscriptions paid before that date will be accepted, regardless of the amount of increase in the postal rates. But, of course, we may be forced to ask for a higher rate in the case of membership and subscription renewals made after July 1, 1974. Similarly, the handling charges on the various items will, no doubt, have to be increased to cover the increased fees charged by the postal service.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U.S.A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

W. S. M.

The Seventh Annual Meeting of the Western Society of Malacologists will be held June 19 to 22, 1974, at the Kellogg West Conference Center on the campus of California State Polytechnic College, Pomona, California. The program will feature contributed papers, symposia, displays, and study workshops on molluscan subjects. In addition to the program of research papers, there will be a concurrently scheduled program of popular presentations on shells or shell collecting.

Inquiries about the meeting should be made no later than May 15th and should be directed to the Secretary, Mrs. Edith Abbott, 1264 West Cienega Avenue, San Dimas, California 91773. Applications for membership should be sent to the Treasurer, Mr. Bertram C. Draper, 8511 Bleriot Avenue, Los Angeles, California 90045. Dues are $5.00 for regular members, $1.00 for additional family members, and $2.00 for students. Regular members and students receive the annual publication of the Society, The Echo.

Executive Board members for the year are: President Dr. James H. McLean; First Vice-President Dr. George Radwin; Second Vice-President Dr. Judith Terry Smith; Secretary Mrs. Edith Abbott; Treasurer Mr. Bertram C. Draper; Members at Large Dr. Vida Kenk and Mr. Barry Roth; the three most recent Past Presidents are Dr. Eugene Coan, Mrs. Beatrice Burch, and Mrs. Twila Bratcher.

INFORMATION DESK

Differentiation:

The Meaning of ICZN Article 13 (a) (i)

BY

R. V. MELVILLE

Secretary, ICZN, % British Museum (Natural History)
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Dr. Eugene V. Coan's interesting contribution (Coan, 1973) on this subject reveals one of the difficulties in

drawing the line between taxonomy and nomenclature. It also shows that zoologists are themselves responsible in the first place for the clarity and usefulness of their publications.

As I remember, the drafting of Article 13, Section (a), Subsection (i) gave the Editorial Committee appointed by the London (1958) International Congress of Zoology no small difficulty. No doubt the existing wording could be altered to solve the problems of some, but probably only at the cost of creating problems for others. Requirements vary from one group to another. It may well be impossible to draft a description of a new "large, pink murex" from the Panamic province that would by itself differentiate a new taxon. On the other hand, I have read descriptions of belemnites (SWINNERTON, 1936 - 1955) which enable the reader to visualize clearly in the mind's eye how each species differs in form from those nearest to it: and belemnites are not the most promising objects from this point of view. Thus, to impose a more explicit and rigid requirement might be thought not only unduly paternalistic, but also an infringement of taxonomic freedom.

I sometimes wonder how much use zoologists make of the Appendices to the Code. Dr. Coan's point (1), for instance, is well represented by Appendix E 1: "A zoologist, when drawing up the description of a new taxon, should include comparisons with related taxa such as will assist later identification of the taxon". His point (4) is covered by Appendix E 17: "The description of a new taxon of the species-group should be accompanied by a satisfactory illustration or by a bibliographic reference to such an illustration". Note that it is appropriate for the word "satisfactory" to appear in this Recommendation, whereas it would be pointless to include it in the mandatory text of Article 13 (a) (i).

Dr. Coan rightly points out that the difficulties alleged against this provision are in fact arguments in favour of the best comparisons possible. It is also true, in my experience, that the one vital comparison one hopes to find is always the one that is not made! But we cannot expect all our difficulties to have been anticipated for us.

It seems to me that, in the final resort, the interpretation of Article 13 (a) (i) is a matter for the conscience of the individual zoologist. I should be inclined to oppose any proposal to strengthen the mandatory wording of the Article or to introduce yet another starting date into the Code. Moreover, I think it would be inappropriate for the Code to refer, even in a Recommendation, to the standard of knowledge or expertise that should be attained by a zoologist describing a new taxon. On the other hand, Dr. Coan's point (2) is well taken, and I think there is a good case for adding this to Appendix E to the Code.

Literature Cited

COAN, EUGENE VICTOR
1973. Differentiation: The meaning of ICZN Article 13 (a) (i). The Veliger 16 (2): 243 - 245 (1 October 1973)
SWINNERTON, H. H.
1936-1955. A monograph of British Cretaceous belemnites. Palaeontogr. Soc., xl+86 pp.; 18 plts.

BOOKS, PERIODICALS, PAMPHLETS

Seashore Life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago

by EUGENE N. KOZLOFF, University of Washington Press, 1973; illustrated, ix+282 pp. and 28 color plates; cloth, $15.00; paper, $6.95

This book, by the able biologist Eugene Kozloff, presents an excellent picture, for the beginner or non-specialist, of the shallow-water marine life of the sheltered waters of the Puget Sound area. In scope and quality it compares favorably with the smaller books on "*Seashore Life*" of the northern and southern Californian coasts by Joel Hedgpeth and Sam Hinton, respectively (Univ. of Calif. Press), but covers both a more northerly and a more protected region than those treated by the latter authors. Kozloff's approach differs from theirs in being by way of typical environmental situations or habitats, namely floats and pilings, rocky shores, sandy beaches, and quiet bays, for each of which he describes the distinctive and common plants and animals. In this respect his book follows the tradition of Ricketts and Calvin in their well-known "*Between Pacific Tides*" (Stanford Univ. Press), although Kozloff's book is considerably less inclusive. Plants as well as animals are covered, and Kozloff succeeds in presenting a well-balanced picture. For the specialist reader of The Veliger, or the single-minded shell collector, the book offers little – it is written in non-technical language at a high level of accuracy, but it is clearly addressed to non-specialists, to beginning students in marine biology, and to the general public. To the professional biologist visiting the Puget Sound area for the first time it offers an easy and attractive overview; to the beginning biology student or the intelligent family vacationing in the Puget Sound area it offers a nicely-balanced picture of marine life that could hardly fail to stimulate interest and answer many questions. It is in general very well illustrated, except that a few of the photographs should, and hopefully will, be replaced by clearer ones in a subsequent reprinting.

Ralph I. Smith

A Marine Invertebrate Faunule from the Lindavista Formation, San Diego, California

by George L. Kennedy, Trans. San Diego Soc. Nat. Hist. vol. 17, no. 10, pp. 119 - 128, 1 fig. (of fossils). 28 March 1973

The first molluscan fossils from the Lindavista Formation, a unit that caps a broad coastal terrace extending from northeasternmost Baja California northward to Oceanside, California, indicate an early Pleistocene age and clear up a long standing controversy over its age. The critical species, *Arca sisquocensis* and *Pecten bellus,* are not known to occur in strata younger than early Pleistocene. The small assemblage is inferred to represent a mixture of species from very shallow sandy beach and cobbly substrates. Some of the mollusks are illustrated.

W. O. Addicott

Early Pliocene Marine Climate and Environment of the Eastern Ventura Basin, Southern California

by J. Philip Kern, Univ. of Calif. Publ. Geol. Sciences, vol. 96, 117 pp.; 30 March 1973

A diverse molluscan fauna of early Pliocene age from the eastern part of the Ventura Basin, southern California, represents a fully marine environment and depths of about 18 to 54m. An unusually thorough biogeographic analysis of this fauna shows that marine surface water temperatures during the late Pliocene were somewhat warmer than today, contrary to earlier postulates of significantly warmer water temperatures. Kern has refined techniques utilized by earlier students of late Tertiary marine paleoclimatology by dealing with temperature critical to reproduction and maintenance of species populations rather than survival temperatures. He has also shown that certain species have changed their temperature tolerance since the Pliocene. A systematic catalogue of the molluscan fauna is included.

W. O. Addicott

Marine Paleoclimatology and Paleoecology of a Pleistocene Invertebrate Fauna from Amchitka Island, Aleutian Islands, Alaska

by Richard C. Allison, Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 13, pp. 15 - 48. Elsevier Scientif. Publ. Comp., Amsterdam

This treatment of the moderately large molluscan fauna is of special interest because Allison has carefully evaluated 6 different methods of determining marine surface water temperature at the time of deposition. The methods that appear to be most reliable utilize biogeographic data and oxygen isotope ratios. They indicate winter minimum and summer maximum temperatures about the same as present-day ones. Based upon the essentially modern aspect of the faunal assemblage and radiometric ages of about 130 000 years, this fauna has been assigned to the late Pleistocene.

W. O. Addicott

Geology and Paleontology of Canal Zone and Adjoining Parts of Panama; Description of Tertiary Mollusks (Additions to Gastropods, Scaphopods, Pelecypods: Nuculidae to Malleidae)

by Wendell P. Woodring, U. S. Geol. Survey Prof. Paper 306-E, pp. 453-539, plts. 67 - 82, 1973. $1.75 from Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402

The penultimate chapter in Woodring's monograph of the Canal Zone mollusks increases the described fauna to some 550 species and subspecies. About 125 species remain to be treated. Most of the species are from the middle Miocene Gatun Formation, as has been the case with previous chapters. The known fauna of this formation now numbers about 330 species. Other species are described from formations of late Eocene to early Miocene age. Among the pelecypods the family Arcidae is extremely diverse taxonomically. The largest of the 6 Arcid genera, *Anadara* includes 25 species and 6 subgenera. Species of the subgenus *Grandiarca* are divided into brackish water and marine groups. As in earlier chapters, the plates of illustrations of fossils are of exceptionally high quality.

W. O. Addicott

The Neogene of Kamchatka

by Yuri B. Gladenkov, Acad. Sci. of U. S. S. R., Trans. Geol. Inst., vol. 214, 252 pp., 8 plts., Moscow, 1972 [in Russian]

A new zonation of the middle and late Tertiary of the Kamchatka Peninsula and nearby North Pacific regions based upon species of *Yoldia* is set forth in this comprehensive report. Ten successive *Yoldia* zones of Oligocene to late Pliocene age are described and are shown to be useful in North Pacific correlation. They are based upon the author's detailed biostratigraphic work on the Neogene sequence of Karaginskiy Island situated off the northeastern coast of Kamchatka. Species of *Yoldia* which are placed in 6 subgenera: *Yoldia* s. s., *Cnesterium, Port-*

landella, Megayoldia, and *Multidentata.* Gladenkov includes a comprehensive synthesis of paleontological and biostratigraphic investigations on the Kamchatka Neogene and comments on the relationship of the Kamchatka Neogene to coeval Japanese and west North American faunal sequences. A section on the modern North Pacific molluscan fauna includes discussion of the trophic zonation of benthic mollusks, amphipacific dispersal of certain molluscan taxa, and benthic invertebrate communities of the Bering Sea.

W. O. Addicott

Common Intertidal Invertebrates of the Gulf of California

by Richard C. Brusca. 427 pp., illust.; Univ. Arizona Press, paper, $10.95. July 1973

We quote from the preface:
"This handbook is the first publication of comprehensive taxonomic keys and species characterizations for the intertidal fauna of the Gulf of California. It is designed for use by students, teachers, and interested amateurs, ... " In a general way, this book is quite satisfactory; it is well printed, the illustrations, for the most part, are excellent. The keys seem to be easily used. Obviously, this book will be handy and useful in the field and will be welcomed especially by serious amateurs who wish to become better acquainted with the wealth of animal forms that can be encountered in the Gulf of California.

From a slightly different viewpoint, there seem to be some minor flaws. Aside from some limited coverages – which are obviously unavoidable in a book of this type and with which we do not find fault – there is a tendency of a colloquial use of the English language. Since the book is intended for the use of *students*, terms should be used correctly and precisely. Perhaps we have a "thing" about the word "intertidal". Dictionaries we have checked do not include this word as a noun. Therefore, animals should be reported as found in "the high intertidal zone" rather than "in the high intertidal." However, in general this book can be recommended highly, assuming that some of the typographical errors will be corrected in the many future editions this relatively inexpensive handbook really deserves.

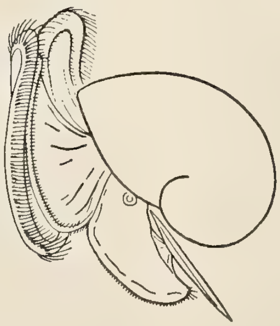
R. Stohler

Reef and Beach Life of New Zealand

by Michael Miller and Gary Batt. 141 pp., richly illustrated with black and white and color reproductions. Collins Bros. & Co. Ltd., P. O. Box 1, Auckland, New Zealand. $NZ9.80. 24 October 1973

An excellent introduction to the shores of New Zealand is provided in this book. It is obviously addressed to the seriously interested novice marine biologist as it explains in easily understood terms about the strange phenomena of high and low tides. In addition, the interrelation between animals and plants in the intertidal area is clearly shown. For the malacologist, the many excellent photographs of living mollusks are of great interest and the shell collector will be able to find many of his prized possessions correctly named. However, all the "neighbors" of the mollusks (that is a little exaggerated, as the scope of the book could not possibly cover ALL) are also considered. Of course, from the point of view of specialists in non-malacological disciplines, the mollusks treated in this volume will be the "neighbors" of their special pets. What we are trying to convey is that this is a well rounded presentation of what the title of the book promises. We like it!

R. Stohler



THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.